



## CHAPTER 6

### A SPECIES LEVEL ANALYSIS OF THE EFFECT OF HERBIVORES AND MAN ON THE SAND FOREST VEGETATION OF MAPUTALAND, NORTHERN KWAZULU-NATAL, SOUTH AFRICA

#### Abstract

Sand Forest in the northern Maputaland region of KwaZulu-Natal in South Africa is deemed the most valuable, but also probably the most complex vegetation type of this part of the Maputaland – Pondoland – Albany hotspot of biodiversity. Its structure and dynamics have been provisionally described but the descriptions remain mostly speculative. The current human population growth in that region called for an in-depth investigation of the forest structure and dynamics in order to evaluate the most successful conservation options available. It appears that Sand Forest is a complex assemblage of at least three tree communities defined by different canopy and subcanopy levels. It is dominated by fine-grained species with an ideal population structure (inverse J-shaped) and therefore can be considered a fine-grained forest. The three communities appear to define a gradient in grain and may represent successional stages of the Sand Forest sub-association as a whole. The forest regeneration appears dependent on the creation of small canopy gaps either by natural processes or elephants, while the creation of large gaps seems to lead to a successional change to woodland. Management of conservation areas where Sand Forest occurs should therefore concentrate efforts on regulating animal populations to levels that provide gap properties that favour forest regeneration.

#### Keywords

Elephant, fine-grain forest, gaps, Sand Forest, size class distribution, succession, vegetation dynamics

#### Introduction

The structure and dynamics of African forests remain relatively poorly documented. The number of long-term studies on large plots, allowing a good understanding of forest dynamics and structure is limited to a few sites in Central and East Africa (Condit 1995; Hitimana *et al.* 2004; Ndangalasi *et al.* 2007). In general, information is most often gathered through a single survey, describing size class frequencies (Condit *et al.* 1998; Obiri *et al.* 2002), which provide a largely static representation of the plant populations at the time of study. To gain an understanding



of dynamics, repeated surveys would be needed (Obiri *et al.* 2002; Lawes and Obiri 2003).

Because such punctual surveys are often the only source of information available (Obiri *et al.* 2002; Lawes and Obiri 2003; Niklas *et al.* 2003), a range of techniques have been devised to derive as much knowledge as possible from simple size class distributions. These techniques range from fitting a regression slope to the size class distributions and discussing the steepness of the slope (Poorter *et al.* 1996; Lykke 1998; Lawes and Obiri 2003; Niklas *et al.* 2003), evaluating the position of the mean diameter of the population (Niklas *et al.* 2003), and determining the grain of forests and species (Midgley *et al.* 1990; Everard *et al.* 1994; Everard *et al.* 1995; Obiri *et al.* 2002; Lawes and Obiri 2003). Although these methods do not replace long-term studies, the combination of these methods allows forestry practitioners to make some inferences on population dynamics (Obiri *et al.* 2002; Lawes and Obiri 2003; Niklas *et al.* 2003; Boudreau *et al.* 2005).

The importance of such analyses is emphasised by the traditional value of forests for poor rural people. Rural people utilise forests freely to obtain a large range of products, thereby saving the few cash resources for other uses (Madubansi and Shackleton 2006; Shackleton *et al.* 2007). Even in South Africa where alternative sources of energy have been provided to rural households, the contribution of firewood for heating and cooking has remained unchanged, while the new energy has been used for luxury items (Madubansi and Shackleton 2006; Shackleton and Shackleton 2006; Madubansi and Shackleton 2007). Despite such government programmes for development in the more advanced countries, the utilisation of natural resources by rural people remains essential to survival, and in areas of high demographic growth the sustainability of resources becomes questionable (Shackleton 1993; Banks *et al.* 1996; Shackleton 1998; Emanuel *et al.* 2005; Shackleton *et al.* 2005). In these areas, valuing the wealth represented by the resource base is essential, but understanding the limits imposed by the dynamics of the resource base is critical to ensure its future (Obiri *et al.* 2002; Lawes and Obiri 2003; Boudreau and Lawes 2005; Boudreau *et al.* 2005; Emanuel *et al.* 2005; Pote *et al.* 2006).

In Maputaland, the trend in demographic growth is upwards (Kloppers 2001; Matthews 2006; Peteers 2005; Jones 2006) and while resource utilisation until present appears, for the most part, to have been limited (Brookes 2004; Gaugris *et al.* 2004; Gaugris *et al.* 2007), it has become clear that the modernisation of society is shifting the utilisation patterns towards increased clearing of land for the creation of new households as the number of residents per households decreases (Peteers 2005).



Additionally, in the past six years Maputaland has emerged as a new tourism destination in South Africa, and therefore the natural demographic growth in the region is likely to be increased by immigration of people towards the economic hubs of Maputaland to benefit from tourism-related activities (Matthews 2006; Peteers 2005). The present state of affairs calls for an evaluation of the natural resource base, and its dynamics.

The study area encompasses two sites in the remote, rural, and poor northern Maputaland region of KwaZulu-Natal in South Africa ( $-26.85^{\circ}$  to  $-27.15^{\circ}$  South and  $032.35^{\circ}$  to  $032.60^{\circ}$  East). Site one is located in Tembe Elephant Park (Tembe), site two in the neighbouring Manqakulane rural community (6 km south of the southern fence of Tembe), where the Tshanini Community Conservation Area lies (Tshanini). These selection of these two sites allowed an analysis of the effect of herbivores, especially the African elephant *Loxodonta africana* (Blumenbach 1797), on individual tree species by comparing Tembe (with herbivores) to a control area (Tshanini) where utilisation by people and herbivores was low to nil (Gaugris *et al.* 2004).

The effect of herbivores on Sand Forest is a much-debated topic since the late 1990s, but it is undermined by a blatant lack of reliable and in-depth information on the Sand Forest structure and dynamics. Despite being a unique, valuable and important vegetation type, Sand Forest remains a poorly documented forest type in South Africa. The sum of recent available knowledge on this vegetation unit rests on a cumulative total of 31 plots (5 + 8 + 18 plots) surveyed by three separate studies (Matthews *et al.* 1999; Matthews *et al.* 2001; Gaugris and Van Rooyen In Press). The need for additional knowledge is essential for understanding the structure and dynamics of such a special vegetation type, and the influence that animals may have.

In the present study, the objectives were to present new and more extensive information on the Sand Forest structure, but also to discuss the potential effect of herbivores. To present these aspects, the size class distributions of woody species from the Sand Forest vegetation, under differing utilisation regimes during the 15 years prior to the present study, were evaluated. The range of techniques available for single surveys were utilised and expanded to present the woody species population structures at both sites, but also to compare them between sites and evaluate the influence of herbivores on the woody species population structure. It is hoped that these comparisons will allow a better understanding of the influence of herbivores on the sensitive Sand Forest.



## Study area

The study area is situated in the Maputaland coastal plain at nearly equal distance from the sea to the east and the Lebombo Mountain Range to the west. The Maputaland coastal plain consists of a sandy plain interspersed with ancient littoral dunes, vegetated by open to closed woodlands, with patches of the rare Sand Forest vegetation. The Muzi Swamp runs along the eastern side of the study area (Matthews *et al.* 2001; Gaugris *et al.* 2004). The region experiences hot, wet, and humid summers, while winters are cool to warm and dry. The mean annual rainfall for the region was 721 mm in the period from 1981 to 2003 (Matthews 2006).

The creation of Tembe in 1983 stemmed from a desire to conserve the region's remaining wildlife and protect the biodiversity rich Sand Forest vegetation from utilisation by people. The park's 30 000 ha were fenced in two stages, the South African sides in 1983, followed by the northern border with Mozambique in 1989. The conservation policy for Tembe has been one of low tourism development, and the park's main purpose was to preserve the region's rare vegetation and wildlife rather than attract mass tourism (KwaZulu-Natal — Nature Conservation Services 1997; Browning 2000). As a consequence, Tembe has received little tourism for most of its lifespan and the conservation principle has been criticised as it does not provide enough economic returns for the neighbouring communities. A thorough description of Tembe appears in Matthews *et al.* (2001).

Tshanini Game Reserve was established in 2000 on the western 2 420 ha section of tribal land of the Manqakulane Community. It was renamed Tshanini Community Conservation Area and gazetted in December 2005. Until 1992 this land was used by the people, supplying them with building material, firewood, grazing and hunting grounds, fruit and honey, while some areas on the eastern side were cleared for subsistence cultivation. However, in 1992, the people moved eastwards to the Muzi Swamp area where a government-installed water supply and better soils promised an easier life (Gaugris 2004). Tshanini has been relatively untouched since that date, protected by the people's desire to turn it into a conservation area (Gaugris *et al.* 2004). Tshanini is fully described in Gaugris *et al.* (2004).

A total of five Sand Forest vegetation units were sampled in the two study sites (Table 1). Three new vegetation types were sampled in Tembe, namely a new type of Sand Forest vegetation (presented in Chapter 4 of the present study), and the *Afzelia quanzensis* clumps and *Afzelia quanzensis* forest. The latter two are not described by Matthews *et al.* (2001) or Gaugris *et al.* (2004), and expert opinion was used to name them, despite the lack of data to prove their status adequately.

Table 1: Sand Forest types of the study area in Maputaland, northern KwaZulu-Natal, South Africa

Code	Abbreviation	Community name	Synonym in other studies
1		Sand Forest association	
1.1	AQ	<i>Azelia quanzensis</i> subassociation	Newly described in the present study
1.1.1	AQC	<i>Azelia quanzensis</i> clumps	Newly described in the present study
1.1.2	AQF	<i>Azelia quanzensis</i> forest	Newly described in the present study
1.2	SF	Sand Forest association	
1.2.1	SSF	Short Sand Forest	Short Sand Forest in Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)
1.2.2	ISF	Intermediate Sand Forest	Tall Sand Forest in Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)
1.2.3	TSF	Tall Sand Forest	Newly described in the present study, replaces TSF of Matthews <i>et al.</i> (2001) and Gaugris <i>et al.</i> (2004)



## Methods

In the present study, rectangular plots of varying length and width, depending on the vegetation density, were used to obtain abundance and size class distribution data of tree species in the two sites studied. A total of 254 plots were surveyed in the region, of which 59 plots were sampled in the Sand Forest in Tembe and 18 plots in that of Tshanini. The data were captured in Microsoft Excel spreadsheets and then compiled into a Microsoft Access database.

A classic species based size class distribution regression analysis on the spread of stem diameter values of woody plants (hereafter referred to as the SCD analysis) in each vegetation unit was conducted. The limitations of such analyses for obtaining information on population dynamics are acknowledged (Condit *et al.* 1998; Niklas *et al.* 2003). However, it is expected that the range of other factors evaluated in the present study, such as centroid location, contribution of smaller size classes, subcanopy and canopy densities, frequency, and the fact that two study sites are compared, one of which is considered a control area, will contribute to a much improved insight in the species population structure and possibly dynamics of Sand Forest vegetation.

Stem diameter measurements of woody plants (for multi-stemmed individuals only the largest stem diameter was included for calculations) were classified into 12 size classes of varying diameter width measured in centimetres (>0 to <1 cm, 1 to <2 cm, 2 to <4 cm, 4 to <6 cm, 6 to <10 cm, 10 to <14 cm, 14 to <20 cm, 20 to <26 cm, 26 to <34 cm, 34 to <42 cm, 42 to <52 cm,  $\geq$  52 cm). The variations in diameter segments were used to accommodate approximately equal numbers of individuals in each size class with increasing size because the number of individuals generally declines with size (Condit *et al.* 1998; Lykke 1998). The size classes were selected after a careful review of the stem diameters observed in the region (Brookes 2004; Gaugris 2004; Gaugris and Van Rooyen In Press).

The number of individuals in each size class is divided by the width of the class to obtain a mean number of individuals per diameter unit in each class (Condit *et al.* 1998) before calculating the density ( $D_i$ ) per size class per vegetation unit per species in each study site. The stem density per species per vegetation unit was calculated to reflect species frequency in the plots to avoid the density dilution observed in habitat density calculations (Lawes and Obiri 2003). The class midpoint ( $M_i$ ) was set as the halfway measurement for each size class for each diameter size class (Condit *et al.* 1998).



Once  $D_i$  and  $M_i$  were established, normal logarithmic transformations (Condit *et al.* 1998) of the type  $\ln(D_i+1)$  and  $\ln(M_i+1)$  were used to standardize the data (Niklas *et al.* 2003) before calculating the least square linear regressions fitting the data. The value of 1 was added as some size classes' bins were not represented (Lykke 1998). The regressions were calculated with  $\ln(M_i+1)$  values as the independent variable and  $\ln(D_i+1)$  values as the dependent variable (Condit *et al.* 1998; Lykke 1998). The slopes of these regressions are referred to as SCD slopes.

The minimum number of individuals sampled to perform a reliable regression analysis was set at 30 (hereafter referred to as the full analysis) (Niklas *et al.* 2003). Regressions were also calculated for species with a sampled number of individual comprised from 10 to 29 (hereafter referred to as the limited analysis) as some authors consider it a sufficient sample size (Condit *et al.* 1998; Lykke 1998). However, these species are treated separately and greater attention is paid to the significance of  $F$  and the  $r^2$  values when they are considered. Diameter size classes up to the largest size class with individuals present are included in the regressions; larger, empty size classes are omitted. For each regression, the site, vegetation unit, species, slope, Y-axis intercept,  $r^2$  value, significance of  $F$ , number of size classes over which the regression was calculated and the number of individuals sampled are indicated.

A link has been established between the position of the mean diameter of the species population structure, termed "centroid", and the size class distribution midpoint. A centroid skewed to the left of the midpoint indicates a young and growing population, whereas one skewed to the right indicates an older, relatively undisturbed population (Niklas *et al.* 2003). In the present study, the centroid is calculated in two ways. Centroid 1 represents the centroid position when the whole data set including all 12 size classes is analysed; whereas centroid 2 is calculated on a data set restricted to size classes ranging from 3 to 12 to remove the potential effect of weather on seedling germination. The species size class distribution centroid (centroid 1) represents the mean diameter at the species population level, and the diameter size class in which it is located is therefore indicated (Niklas *et al.* 2003). The location of centroid 2 is more meaningful, as it establishes the mean diameter of the established tree strata (Niklas *et al.* 2003). The magnitude of the shift from centroid 1 to centroid 2 indicates the relative importance of small individuals at the time of the study.

The subcanopy and canopy densities per species were also calculated. In the present study, these correspond to the sum of densities per species for the size classes 3 to 6 for the subcanopy category, thereby removing all the seedlings and saplings from the analysis, and the size classes 7 to 12 for the canopy category. The





frequency of occurrence for each species in each vegetation unit was calculated as the percentage of plots in which it occurred per vegetation unit (Lawes and Obiri 2003). The use of subcanopy and canopy densities, associated with the frequency of occurrence allows the determination of species grain.

The graphical model of Lawes and Obiri (2003) to determine the grain of species by plotting canopy density on the X-axis and subcanopy density on the Y-axis, is used to define which species are fine, coarse, or intermediate-grained. The model appears in Figure 1, and ln-transformed values were used to facilitate reading due to high densities and large density variations observed in the study area sites. The same critical lower bounds for canopy, subcanopy and frequency of occurrence levels as Lawes and Obiri (2003) were used. These authors evaluated a range of forests from the Eastern Cape and KwaZulu-Natal provinces of South Africa using this model, and it was deemed judicious to use the same limits to allow comparison at the regional level. These boundaries were 10 and 30 individuals per ha for the canopy and subcanopy levels respectively, and a minimum of 50% frequency of occurrence in the sampled plots for a species to be considered fit for selection in the model. Grain is further determined by the position of species in the scatter plot within the above boundaries, and the relative position above (intermediate to fine-grain) or below (intermediate to coarse-grain) a line that represents equal densities at canopy and subcanopy levels. Frequency of occurrence was not represented graphically as it was already provided in the previous analysis.

A convenient grouping of the species in three Types depending on the steepness of the slope is presented. The Types are:

- Type 1, species with slopes steeper or equal to half that of the vegetation unit (calculated on all individuals of all species, see Chapter 5) evaluated in the particular utilisation regime. These species show good regeneration.
- Type 2, species with slopes shallower than half that of the vegetation unit evaluated in the particular utilisation regime, but steeper than a threshold fixed at a slope coefficient of -0.15 (Lykke 1998).
- Type 3, species with slopes shallower than the above threshold or with positive slope coefficients.

Finally, the slopes and Y-axis intercepts of regressions were compared for species found within the same vegetation unit but under different utilisation regimes by means of an analysis of covariance (ANCOVA) by using the GraphPad PRISM 4 software (Windows version, GraphPad Software, San Diego California USA, [www.graphpad.com](http://www.graphpad.com)). This analysis first compares the regressions slopes, and should





there be no significant difference between slopes, the Y-axis intercepts are then compared. When slopes are similar, a pooled slope value is given, and when Y-axis intercepts are similar, a pooled Y-axis intercept value is presented. Should there be no significant difference at either slope or Y-axis intercept levels, the species present in the two sites, can be described through the pooled slope and Y-axis intercept.

## Results

In Tshanini 79 woody species were inventoried and in Tembe 105 species. A total of 57 Sand Forest woody species met the criterion for analysis with 55 of these found within the Intermediate Sand Forest, while 33 of them were recorded in the Short Sand Forest.

### *Short Sand Forest*

A total of 22 species were analysed in the Short Sand Forest in Tshanini (Table 2). The species from the full analysis in general had steep slopes, with only 12.50% of species with a flat or positive slope coefficient (*Monodora junodii* and *Boscia filipes*). Important species for household buildings, such as *Brachylaena huillensis* or *Ptaeroxylon obliquum* (Gaugris *et al.* 2007) had steep slope coefficients. However, while the latter species was ubiquitous in this vegetation unit and occurs in great abundance in the subcanopy and canopy levels, the former species was relatively rare (33.33% frequency of occurrence, Table 2) and was only found in the subcanopy.

The most abundant species in the subcanopy in this vegetation unit in Tshanini appeared to be *Hymenocardia ulmoides*, followed by *Psydrax locuples*, while the canopy stratum was dominated by a mixture of *Dialium schlechteri*, *Ptaeroxylon obliquum* and *Pteleopsis myrtifolia*. The first mentioned can grow into a fairly large tree (Pooley 1997), and represents the most abundant large tree found in the canopy. The other large canopy tree is *Cleistanthus schlechteri*, although it was found at much lower densities in the canopy. In general, most species found at both canopy and subcanopy levels showed a pyramidal structure whereby the subcanopy density was greater than the canopy density.

In the limited analysis, three species of shrubs showed a shallow or positive slope coefficient, denoting struggling populations (Table 2). *Spirostachys africana* is a woodland species (Pooley 1997; Gaugris 2004), and its canopy density was also higher than the subcanopy density.

Mean SCD centroid 2 for both full and limited analyses was located within size class 4 (Table 2). Mean centroid 1 was located within size class 3 in the full analysis

Table 2: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the Short Sand Forest in Tshanini Community Conservation Area, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SC range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / ha)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain	
<b>Community Level</b>	<b>Community SCD</b>	<b>-2.37</b>	<b>11.24</b>	<b>0.97</b>	<b>0.52</b>	<b>329.89</b>	<b>**</b>	<b>10</b>	<b>12</b>	<b>2411</b>						
Full	<i>Acalypha glabrata</i>	-1.54	8.18	0.46	1.16	0.85	-	1	3	239	02	03	517	0	50.00	NA
Full	<i>Boscia filipes</i>	-0.13	2.93	0.00	2.05	0.03	-	6	8	48	05	05	733	33	83.33	Fine
Full	<i>Brachylaena huillensis</i>	-2.21	7.29	0.76	0.92	6.22	-	2	4	62	02	04	133	0	33.33	NA
Full	<i>Cleistanthus schlechteri</i>	-0.93	5.12	0.71	0.62	14.78	**	6	8	41	05	05	483	67	16.67	Fine (NA)
Full	<i>Dialium schlechteri</i>	-1.06	5.74	0.58	1.01	9.57	*	7	9	80	05	05	1050	150	83.33	Fine
Full	<i>Drypetes arguta</i>	-1.25	7.13	0.90	0.30	18.63	*	2	4	115	02	03	833	0	100.00	NA
Full	<i>Grewia microthyrsa</i>	-0.55	4.59	0.04	2.10	0.07	-	2	4	41	03	03	250	0	100.00	NA
Full	<i>Hymenocardia ulmoides</i>	-2.71	9.13	0.78	1.58	25.43	**	7	9	298	03	03	3467	17	100.00	Fine
Full	<i>Hyperacanthus microphyllus</i>	-0.95	3.87	0.11	2.62	0.63	-	5	7	57	03	03	767	17	100.00	Fine
Full	<i>Monodora junodii</i>	1.46	1.31	0.27	1.94	1.13	-	3	5	33	04	04	483	0	100.00	NA
Full	<i>Psyrax locuples</i>	-1.91	8.11	0.87	0.81	48.65	**	7	9	205	03	04	2150	100	83.33	Fine
Full	<i>Ptaeroxylon obliquum</i>	-2.17	8.30	0.85	1.02	39.60	**	7	9	508	02	05	483	133	100.00	Fine
Full	<i>Pteleopsis myrtifolia</i>	-1.63	7.08	0.75	1.04	21.34	**	7	9	126	04	04	1567	100	100.00	NA
Full	<i>Salacia leptoclada</i>	-2.88	8.11	0.85	0.88	11.42	-	2	4	77	02	03	300	0	100.00	NA
Full	<i>Toddalopsis bremekampii</i>	-0.88	6.47	0.27	1.16	1.13	-	3	5	153	03	03	1917	0	83.33	NA
Full	<i>Uvaria caffra</i>	-0.55	3.47	0.03	2.73	0.13	-	4	6	44	03	03	500	0	100.00	NA
	Mean SCD centroid location for common species:										03	04				
Limited	<i>Coddia rudis</i>	-1.50	5.75	0.97	0.20	28.16	-	1	3	20	02	03	83	0	66.67	NA
Limited	<i>Croton steenkampianus</i>	4.10	-0.65	0.55	2.59	1.21	-	1	3	17	03	03	100	0	100.00	NA
Limited	<i>Euclea natalensis</i>	-1.46	5.33	0.76	0.81	15.72	*	5	7	29	03	05	117	17	50.00	Fine
Limited	<i>Margaritana discoidea</i>	0.89	1.66	0.13	1.90	0.44	-	3	5	23	04	04	367	0	50.00	NA
Limited	<i>Ochna arborea</i>	0.57	1.99	0.04	2.16	0.14	-	3	5	18	03	03	200	0	83.33	NA
Limited	<i>Spirostachys africana</i>	-0.88	3.95	0.44	1.23	8.01	*	10	12	22	06	08	100	117	50.00	Intermediate
	Mean SCD centroid location for common species:										04	04				
SC	Size Class															
**	Highly significant ( $p \leq 0.01$ )															
*	Significant ( $p \leq 0.05$ )															
-	Not significant ( $p > 0.05$ )															
NA	Not applicable, following the species grain, it indicates that while grain could be determined, the frequency of occurrence is too low to warrant inclusion in the model															



and size class 4 in the limited one. There was no major shift between the positions of mean centroid 1 and 2 in both analyses.

A total of 18 species were analysed in the Short Sand Forest in Tembe (Table 3). The species *Croton pseudopulchellus* and *Cola greewayi* have the highest subcanopy densities, while the latter also had the highest canopy density. *Brachylaena huillensis* was present in most plots (80.00%), at a higher density than in Tshanini. However, *Dialium schlechteri*, *Psydrax locuples* and *Pteleopsis myrtifolia*, were present in greater abundance in Tshanini than in Tembe where they were classified within the restricted analysis, and the SCD curve slope coefficients for the first and second species belonged to Type 3. The subcanopy density for *Dialium schlechteri* was lower than its canopy density.

The species classified in the full analysis all showed steep SCD curve coefficients (100.00% of species within Type 1, Table 4), while 45.50% of species in the limited analysis fell within Type 3. Mean centroid 2 fell within size class 4 in the full analysis and size class 5 in the limited analysis, whereas centroid 1 is located in size class 3 and 5 within the full and limited analyses respectively. There is no major shift between the positions of mean centroid 1 and 2 in both analyses.

A comparison of SCD slope coefficients and Y-axis intercepts between the species found within the full analysis (Table 5) at the two sites showed that out of five species in common, only *Drypetes arguta* showed a significant difference at the Y-axis intercept level, with a higher value for the Tshanini site. No species were shared between the limited analyses (Table 5), while three species (*Dialium schlechteri*, *Psydrax locuples* and *Pteleopsis myrtifolia*) could be compared across analyses (Table 5). The SCD slopes of all three species were significantly different between sites. *Dialium schlechteri* had a positive slope in Tembe, while it was negative and steep in Tshanini, *Psydrax locuples* fell within Type 1 in Tshanini and Type 3 in Tembe, and *Pteleopsis myrtifolia* was classified within Type 1 in Tshanini but in Type 2 in Tembe. This represented a total of eight species compared, four of which showed significant differences in SCD curve shape.

#### *Intermediate Sand Forest*

A total of 36 species were analysed in the Intermediate Sand Forest in Tshanini (Table 6). Most species in the full analysis could be classified within Type 1, with a steep slope (Table 4), while the bulk of species in the limited analysis fell within Types 2 and 3. Mean centroid 2 was located within size class 5 for both analyses, while mean centroid 1 was located within size classes 4 and 5 for the full and limited analyses

Table 3: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the Short Sand Forest in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SCD range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / ha)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain
<b>Community Level</b>	<b>Community SCD</b>	<b>-1.92</b>	<b>9.91</b>	<b>0.98</b>	<b>0.30</b>	<b>646.82</b> **	<b>10</b>	<b>12</b>	<b>850</b>						
Full	<i>Brachylaena huillensis</i>	-1.81	6.53	0.83	0.87	28.41 **	6	8	31	03	05	245	19	80.00	Fine
Full	<i>Cola greenwayi</i>	-1.35	6.59	0.87	0.55	40.22 **	6	8	63	04	05	660	151	60.00	Fine
Full	<i>Croton pseudopulchellus</i>	-2.96	9.90	0.89	0.84	24.93 *	3	5	247	02	03	1264	0	80.00	NA
Full	<i>Drypetes arguta</i>	-1.66	7.04	0.95	0.40	113.92 **	6	8	59	04	05	698	57	70.00	Fine
Full	<i>Hymenocardia ulmoides</i>	-1.54	5.99	0.71	1.02	15.05 **	6	8	31	04	04	453	19	80.00	Fine
Full	<i>Salacia leptoclada</i>	-3.11	8.63	0.90	0.85	26.50 *	3	5	65	02	03	321	0	60.00	NA
Full	<i>Toddalopsis bremekampii</i>	-1.50	6.31	0.74	0.88	13.92 *	5	7	41	03	04	566	19	60.00	Fine
	Mean SCD centroid location for common species:										03	04			
Limited	<i>Dialium schlechteri</i>	0.2	0.73	0.12	0.88	1.37 -	10	12	14	09	09	75	189	80.00	Intermediate
Limited	<i>Drypetes natalensis</i>	-1.1	5.28	0.87	0.50	48.32 **	7	9	24	05	05	245	94	80.00	Fine
Limited	<i>Erythrophleum lasianthum</i>	0.0	0.99	0.00	1.18	0.01 -	10	12	10	09	09	19	151	80.00	Coarse
Limited	<i>Ochna natalitia</i>	-0.4	3.92	0.32	0.53	1.43 -	3	5	12	03	04	189	0	50.00	NA
Limited	<i>Pavetta lanceolata</i>	2.6	0.34	0.50	1.96	2.02 -	2	4	20	03	03	302	0	40.00	NA
Limited	<i>Psyrax locuples</i>	-0.07	2.47	0.00	1.52	0.01 -	4	6	10	04	05	170	0	60.00	NA
Limited	<i>Psyrax obovata</i>	-0.34	3.06	0.04	1.80	0.23 -	6	8	28	05	05	472	38	40.00	Fine (NA)
Limited	<i>Pteleopsis myrtifolia</i>	-0.57	3.96	0.65	0.46	13.10 **	7	9	23	06	06	226	170	90.00	Fine
Limited	<i>Tricalysia junodii</i>	-2.98	7.80	1.00	0.00	0.00 -	0	2	28	01	NA	0	0	60.00	NA
Limited	<i>Tricalysia lanceolata</i>	0.15	2.95	0.00	2.64	0.00 -	2	4	16	03	03	245	0	50.00	NA
Limited	<i>Vepris lanceolata</i>	-1.11	3.81	0.23	1.97	1.51 -	5	7	13	03	05	94	38	30.00	Fine (NA)
	Mean SCD centroid location for common species:										05	05			

SC Size Class

\*\* Highly significant ( $p \leq 0.01$ )

\* Significant ( $p \leq 0.05$ )

- Not significant ( $p > 0.05$ )

NA Not applicable, when behind species grain, it indicates that while grain could be established, the frequency of occurrence precludes inclusion in the model

Table 4: The percentage of species with Type 1 to 3 slopes for the Sand Forest vegetation of Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA), for the full ( $\geq 30$  individuals sampled) and limited (10 - 29 individuals sampled) analyses, Maputaland, northern KwaZulu-Natal, South Africa. The total number of species (No spp) for analyses by vegetation unit or sub-unit is indicated in the top line of each analysis

Analysis	Type	Percentage of species per Type by vegetation units and sites					
		Short Sand Forest		Intermediate Sand Forest		Tall Sand Forest	<i>Afzelia quanzensis</i> clumps
		TCCA	TEP	TCCA	TEP	TEP	TEP
<b>Full</b>	<b>No spp</b> →	16	7	22	21	12	2
		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	50.00	100.00	59.09	80.95	100.00	100.00
	Type 2	37.50	0.00	27.27	9.52	0.00	0.00
	Type 3	12.50	0.00	13.64	9.52	0.00	0.00
<b>Limited</b>	<b>No spp</b> →	6	11	14	14	16	8
		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	33.30	27.27	7.14	35.71	31.25	62.50
	Type 2	16.70	27.27	50.00	21.43	25.00	12.50
	Type 3	50.00	45.45	42.86	42.86	43.75	25.00
<b>Combined</b>	<b>No spp</b> →	22	18	36	35	28	10
		(%)	(%)	(%)	(%)	(%)	(%)
	Type 1	45.45	55.56	38.89	62.86	60.71	70.00
	Type 2	31.82	16.67	36.11	14.29	14.29	10.00
	Type 3	22.73	27.78	25.00	22.86	25.00	20.00

Type 1 slopes steeper or equal to half that of the vegetation unit evaluated

Type 2 slopes shallower than half that of the vegetation unit evaluated but steeper than - 0.15

Type 3 slopes shallower than - 0.15 coefficient or with positive slope coefficients

Table 5: A comparison of size class distribution (SCD) slope coefficients and Y-axis intercepts within species and analyses (F = Full analysis, L = Limited Analysis) in comparable Sand Forest vegetation unit in the study sites Tembe Elephant Park (TEP) and Tshanini Community Conservation Area (TCCA), Maputaland, northern KwaZulu-Natal, South Africa

VT	Vegetation unit	Species	Comparison levels		Slope Comparison				Intercept Comparison				Outcome	Note*				
			Sites compared	Analysis	F value	Df <sub>n</sub>	Df <sub>d</sub>	P value	Pooled slope	F value	Df <sub>n</sub>	Df <sub>d</sub>			P value	Pooled intercept		
VT 01.2.1	Short Sand Forest	<i>Brachylaena huilensis</i>	TEP / TGR	F / F	0.20	-	1	8	0.67	-1.87	0.21	-	1	9	0.66	6.74	Similar	-
		<i>Drypetes arguta</i>	TEP / TGR	F / F	1.06	-	1	8	0.33	-1.60	5.29	*	1	9	0.05	-	Different	-
		<i>Hymenocardia uimoides</i>	TEP / TGR	F / F	2.77	-	1	13	0.12	-2.20	1.39	-	1	14	0.26	7.69	Similar	-
		<i>Salacia leptoclada</i>	TEP / TGR	F / F	0.05	-	1	5	0.83	-3.03	0.20	-	1	6	0.67	8.41	Similar	-
		<i>Toddalopsis bremekampii</i>	TEP / TGR	F / F	0.56	-	1	8	0.48	-1.32	3.33	-	1	9	0.10	6.44	Similar	-
		<i>Dialium schlechteri</i>	TEP / TGR	L / F	11.15	**	1	17	<0.01	-	-	-	-	-	-	-	Different	X
		<i>Psydrax locuples</i>	TEP / TGR	L / F	6.40	*	1	11	0.03	-	-	-	-	-	-	-	Different	X
		<i>Pteleopsis myrtiolia</i>	TEP / TGR	L / F	7.58	*	1	14	0.02	-	-	-	-	-	-	-	Different	-
VT 01.2.2	Intermediate Sand Forest	<i>Brachylaena huilensis</i>	TEP / TGR	F / F	0.58	-	1	13	0.46	-1.55	29.11	**	1	14	<0.01	-	Different	-
		<i>Cleistanthus schlechteri</i>	TEP / TGR	F / F	0.05	-	1	19	0.82	-0.44	0.19	-	1	20	0.66	3.13	Similar	-
		<i>Cola greenwayi</i>	TEP / TGR	F / F	7.91	*	1	16	0.01	-	-	-	-	-	-	-	Different	-
		<i>Croton pseudopulchellus</i>	TEP / TGR	F / F	5.51	*	1	10	0.04	-	-	-	-	-	-	-	Different	-
		<i>Dialium schlechteri</i>	TEP / TGR	F / F	28.13	**	1	19	<0.01	-	-	-	-	-	-	-	Different	-
		<i>Drypetes arguta</i>	TEP / TGR	F / F	1.06	-	1	11	0.32	-1.90	1.17	-	1	12	0.30	7.37	Similar	-
		<i>Haplocoelum lololosum</i>	TEP / TGR	F / F	0.55	-	1	17	0.47	-1.02	0.59	-	1	18	0.45	4.04	Similar	-
		<i>Hymenocardia uimoides</i>	TEP / TGR	F / F	1.20	-	1	16	0.29	-1.61	1.64	-	1	17	0.22	6.25	Similar	-
		<i>Hyperacanthus microphyllus</i>	TEP / TGR	F / F	0.97	-	1	10	0.35	-0.82	4.14	-	1	11	0.07	3.62	Similar	-
		<i>Monodora junodii</i>	TEP / TGR	F / F	0.02	-	1	9	0.88	0.30	0.14	-	1	10	0.72	1.34	Similar	-
		<i>Newtonia hildebrandtii</i>	TEP / TGR	F / F	2.22	-	1	20	0.15	-0.06	0.22	-	1	21	0.64	1.02	Similar	-
		<i>Ptaeroxylon obliquum</i>	TEP / TGR	F / F	2.94	-	1	16	0.11	-1.18	5.08	*	1	17	0.04	-	Different	-
		<i>Pteleopsis myrtiolia</i>	TEP / TGR	F / F	0.00	-	1	16	0.98	-0.63	0.26	-	1	17	0.62	3.62	Similar	-
		<i>Salacia leptoclada</i>	TEP / TGR	F / F	1.48	-	1	7	0.26	-2.84	0.07	-	1	8	0.80	7.32	Similar	-
		<i>Toddalopsis bremekampii</i>	TEP / TGR	F / F	0.06	-	1	14	0.81	-2.04	0.38	-	1	15	0.55	7.07	Similar	-
		<i>Lvania caffra</i>	TEP / TGR	F / F	0.78	-	1	8	0.40	-1.23	0.01	-	1	9	0.91	4.21	Similar	-
		<i>Balanites maughanii</i>	TEP / TGR	L / L	7.89	*	1	20	0.01	-	-	-	-	-	-	-	Different	-
		<i>Grewia microthysa</i>	TEP / TGR	L / L	0.03	-	1	6	0.87	-0.33	0.00	-	1	7	0.99	2.28	Similar	-
		<i>Zanthoxylum leprieuri</i>	TEP / TGR	L / L	1.79	-	1	8	0.22	-0.43	1.11	-	1	9	0.32	1.97	Similar	-
		<i>Boscia filipes</i>	TEP / TGR	F / L	0.93	-	1	15	0.35	-0.18	1.48	-	1	16	0.24	1.60	Similar	X
<i>Psydrax locuples</i>	TEP / TGR	F / L	3.6	-	1	12	0.08	-1.61	9.97	*	1	13	0.01	-	Different	-		
<i>Strychnos henningsii</i>	TEP / TGR	F / L	2.32	-	1	9	0.16	-0.12	1.03	-	1	10	0.33	1.78	Similar	-		
<i>Suregada zanzibariensis</i>	TEP / TGR	L / F	0.29	-	1	6	0.61	-0.58	0.02	-	1	7	0.89	2.58	Similar	X		

\*\* Highly significant ( $p \leq 0.01$ )

\* Significant ( $p \leq 0.05$ )

- No: significant ( $p > 0.05$ )

Note\* analyses marked with an X were conducted on regression slopes where F was not significant in at least one site

Table 6: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the Intermediate Sand Forest in Tshanini Community Conservation Area, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SC range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / 1a)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain	
<b>Community Level</b>	<b>Community SCD</b>	<b>-1.86</b>	<b>9.21</b>	<b>0.97</b>	<b>0.44</b>	<b>276.21</b>	<b>**</b>	<b>10</b>	<b>12</b>	<b>2883</b>						
Full	<i>Acalypha glabrata</i>	-1.48	5.45	0.52	1.03	2.20	.	2	4	97	02	03	130	0	91.67	NA
Full	<i>Boscia filipes</i>	-0.44	2.47	0.13	1.26	1.03	.	7	9	50	05	05	140	13	58.33	Fine
Full	<i>Brachylaena huillensis</i>	-1.39	4.18	0.87	0.47	27.85	**	4	6	33	03	05	37	0	8.33	NA
Full	<i>Cleistanthus schlechteri</i>	-0.47	3.14	0.49	0.58	8.59	*	9	11	90	07	07	113	143	75.00	Intermediate
Full	<i>Cola greenwayi</i>	-0.30	3.18	0.03	1.84	0.18	.	6	8	172	05	05	490	30	75.00	Fine
Full	<i>Croton pseudopulchellus</i>	-1.22	4.05	0.29	1.73	1.62	.	4	6	68	03	03	127	0	58.33	NA
Full	<i>Dialium schlechteri</i>	-1.01	4.44	0.84	0.53	47.90	**	9	11	96	05	06	160	70	100.00	Fine
Full	<i>Drypetes arguta</i>	-2.13	7.57	0.91	0.67	48.74	**	5	7	392	03	04	560	3	83.33	NA
Full	<i>Euclea natalensis</i>	-1.63	4.53	0.75	0.92	15.19	*	5	7	44	03	05	13	7	75.00	NA
Full	<i>Haplocoelum foliolosum</i>	-1.13	4.37	0.89	0.45	53.94	**	7	9	62	05	06	87	30	75.00	Fine
Full	<i>Hymenocardia ulmoides</i>	-1.72	6.36	0.93	0.53	113.75	**	8	10	197	04	05	393	17	91.67	Fine
Full	<i>Hyperacanthus microphyllus</i>	-1.38	5.25	0.68	0.86	8.37	*	4	6	107	03	04	203	0	100.00	NA
Full	<i>Manilkara concolor</i>	0.35	1.06	0.11	0.97	0.61	.	5	7	35	05	05	103	10	16.67	Fine
Full	<i>Monodora junodii</i>	0.24	1.32	0.04	1.20	0.20	.	5	7	48	05	05	150	3	66.67	NA
Full	<i>Newtonia hildebrandii</i>	0.16	0.40	0.08	0.69	0.84	.	10	12	34	09	09	33	80	58.33	Intermediate
Full	<i>Psyrax locuples</i>	-1.94	6.08	0.94	0.53	88.47	**	6	8	113	03	04	127	3	58.33	NA
Full	<i>Ptaerosylon obliquum</i>	-1.40	5.36	0.99	0.17	745.42	**	8	10	108	04	05	140	33	83.33	Fine
Full	<i>Pteleopsis myrtifolia</i>	-0.64	3.56	0.49	0.76	7.66	*	8	10	90	06	06	190	80	100.00	Fine
Full	<i>Salacia leptoclada</i>	-2.52	6.76	0.87	0.90	25.66	**	4	6	150	02	03	163	0	83.33	NA
Full	<i>Suregada zanzibaniensis</i>	-0.42	2.27	0.08	1.40	0.44	.	5	7	31	04	04	80	3	58.33	NA
Full	<i>Toddalopsis bremekampii</i>	-2.07	7.25	0.89	0.90	70.90	**	9	11	397	03	04	717	3	100.00	NA
Full	<i>Uvaria caffra</i>	-0.86	3.67	0.21	1.51	1.05	.	4	6	63	03	03	153	0	100.00	NA
Mean SCD centroid location for common species:											04	05				
Limited	<i>Balanites maughamii</i>	0.08	0.28	0.06	0.38	0.66	.	10	12	14	10	10	10	37	41.67	Coarse
Limited	<i>Mystrolyon aethiopicum</i>	-0.24	1.67	0.07	0.95	0.43	.	6	8	20	05	05	50	10	66.67	Fine
Limited	<i>Cordia rudis</i>	-1.79	4.60	0.98	0.20	39.31	.	1	3	29	02	03	17	0	50.00	NA
Limited	<i>Grewia microthyrsa</i>	-0.50	2.48	0.10	1.11	0.22	.	2	4	13	03	03	17	0	41.67	NA
Limited	<i>Hippocratea delagoensis</i>	1.08	0.36	0.36	1.19	1.66	.	3	5	29	04	04	93	0	58.33	NA
Limited	<i>Margantaria discoidea</i>	-0.68	2.48	0.57	0.48	4.00	.	3	5	11	04	05	20	0	33.33	NA
Limited	<i>Ochna arborea</i>	-0.11	1.14	0.02	0.78	0.10	.	5	7	10	05	05	27	3	50.00	NA
Limited	<i>Rhus gweinzii</i>	-0.87	2.67	0.81	0.42	21.02	**	5	7	14	04	05	20	3	58.33	NA
Limited	<i>Rothmannia tischeri</i>	-0.07	1.27	0.01	0.79	0.06	.	7	9	24	06	06	50	27	58.33	Fine
Limited	<i>Spirostachys africana</i>	0.19	-0.09	0.26	0.40	3.08	.	9	11	12	08	08	7	33	33.33	Coarse (NA)
Limited	<i>Strychnos henningsii</i>	0.54	0.61	0.20	0.89	0.74	.	3	5	12	04	04	33	0	25.00	NA
Limited	<i>Tarenna floralis</i>	-0.31	2.20	0.15	0.61	0.53	.	3	5	14	03	04	33	0	25.00	NA
Limited	<i>Vitex ferruginea</i>	-0.32	1.61	0.19	0.64	1.19	.	5	7	15	05	05	37	7	33.33	NA
Limited	<i>Zanthoxylum lepreuri</i>	-0.18	1.32	0.04	0.83	0.22	.	5	7	11	04	05	27	3	58.33	NA
Mean SCD centroid location for common species:											05	05				

SC Size Class

\*\* Highly significant ( $p \leq 0.01$ )

\* Significant ( $p \leq 0.05$ )

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- Not significant ( $p > 0.05$ )

NA Not applicable, when behind species grain, it indicates that while grain could be established, the frequency of occurrence precludes inclusion in the model





respectively. There was no major shift between the positions of mean centroid 1 and 2 in both analyses.

Most species in the full analysis had a pyramidal population structure with a subcanopy density of individuals greater than the canopy density, except for *Cleistanthus schlechteri* and *Newtonia hildebrandtii* where the opposite was true (Table 6). This was confirmed in the latter species by the positive curve slope coefficient. The canopy level was dominated by these two species together with *Dialium schlechteri* and *Pteleopsis myrtifolia*, while the subcanopy level was dominated by *Toddaliopsis bremekampii*, *Drypetes arguta* and *Cola greenwayi*.

In the limited analysis, *Balanites maughamii* showed an inverted pyramid population structure, confirmed by a positive SCD slope coefficient, as did *Spirostachys africana*. Most species classified in this analysis had relatively low density values and did not appear much in the canopy level of the forest except for the above-mentioned species.

Large individuals in size class 12 were sampled for both *Balanites maughamii* and *Newtonia hildebrandtii* (Table 6). Large trees classified in size class 11 were found in the populations of *Cleistanthus schlechteri*, *Dialium schlechteri*, and *Toddaliopsis bremekampii*, while trees classified in size class 10 were found for *Hymenocardia ulmoides*, *Ptaeroxylon obliquum* and *Pteleopsis myrtifolia*.

A total of 42 species were analysed in the Intermediate Sand Forest in Tembe (Table 7). The majority of species in the full analysis could be classified into Type 1 (Table 4), while in the limited analysis the majority of species were in Type 3, followed by Type 1. Mean centroid 2 was located within size class 5 for both analyses, while mean centroid 1 was located within size classes 4 and 5 for the full and limited analyses respectively. There was no major shift between the positions of mean centroid 1 and 2 in both analyses.

The subcanopy level of the Intermediate Sand Forest in Tembe (full analysis, Table 7) was dominated by species such as *Croton pseudopulchellus*, *Drypetes arguta*, *Cola greenwayi* and *Hymenocardia ulmoides*. The canopy level was dominated by *Cleistanthus schlechteri*, *Pteleopsis myrtifolia* and *Dialium schlechteri*. Large (size classes 10 and 11) to very large (size class 12) individuals were sampled in a range of species. The population structure of three large canopy trees (*Cleistanthus schlechteri*, *Dialium schlechteri*, *Newtonia hildebrandtii*) of this community showed an inverse pyramid shape; whereby the subcanopy density was lower than the canopy density, but other species showed a regular pyramidal population structure.

Table 7: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the Intermediate Sand Forest in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SC range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / ha)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain
<b>Community Level</b>	<b>Community SCD</b>	<b>-1.87</b>	<b>9.77</b>	<b>0.98</b>	<b>0.36</b>	<b>414.20 **</b>	<b>10</b>	<b>12</b>	<b>4632</b>						
Full	<i>Brachylaena huillensis</i>	-1.59	5.79	0.96	0.41	196.36 **	9	11	123	03	05	125	21	64.86	Fine
Full	<i>Cassipourea mossambicensis</i>	-1.27	4.38	0.88	0.49	44.06 **	6	8	40	04	05	58	9	45.95	NA
Full	<i>Cleistanthus schlechteri</i>	-0.42	3.12	0.54	0.49	11.58 **	10	12	119	07	08	125	222	81.08	Intermediate
Full	<i>Cola greenwayi</i>	-1.84	7.50	0.96	0.45	262.70 **	10	12	461	04	05	703	140	83.78	Fine
Full	<i>Croton pseudopulchellus</i>	-3.33	9.84	0.93	0.97	77.45 **	6	8	1241	02	03	971	3	100.00	NA
Full	<i>Croton steenkampianus</i>	-2.83	6.74	0.85	0.84	5.54 -	1	3	76	02	03	21	0	35.14	NA
Full	<i>Dialium schlechteri</i>	0.15	0.78	0.08	0.63	0.89 -	10	12	59	09	09	24	152	75.68	Coarse
Full	<i>Drypetes arguta</i>	-1.73	7.22	0.90	0.62	52.00 **	6	8	440	04	05	898	46	97.30	Fine
Full	<i>Drypetes natalensis</i>	-1.21	4.75	0.95	0.29	119.69 **	6	8	69	04	05	104	24	54.05	Fine
Full	<i>Haplocoelum foliolosum</i>	-0.91	3.82	0.82	0.57	45.79 **	10	12	47	05	07	46	43	48.65	Fine (NA)
Full	<i>Hymenocardia ulmoides</i>	-1.51	6.13	0.95	0.42	138.10 **	8	10	197	04	05	332	79	81.08	Fine
Full	<i>Hyperacanthus microphyllus</i>	-0.51	2.50	0.14	1.44	0.97 -	6	8	41	04	04	107	6	54.05	NA
Full	<i>Leptactinia delagoensis</i>	-1.42	4.61	0.53	1.10	3.33 -	3	5	47	03	03	88	0	40.54	NA
Full	<i>Monodora junodii</i>	0.31	1.34	0.07	1.23	0.30 -	4	6	36	04	04	100	0	40.54	NA
Full	<i>Newtonia hildebrandtii</i>	-0.27	1.65	0.12	0.92	1.38 -	10	12	41	10	11	6	100	56.76	Coarse
Full	<i>Psydrax obovata</i>	-0.60	3.52	0.48	0.65	5.65 -	6	8	73	05	06	137	43	48.65	Fine (NA)
Full	<i>Ptaeroxylon obliquum</i>	-0.96	3.75	0.65	0.83	14.68 **	8	10	57	04	06	64	30	72.97	Fine
Full	<i>Pteleopsis myrtifolia</i>	-0.63	3.69	0.60	0.60	11.83 **	8	10	100	06	07	88	164	70.27	Intermediate
Full	<i>Salacia leptoclada</i>	-3.37	8.10	0.96	0.58	67.92 **	3	5	200	02	03	100	0	78.38	NA
Full	<i>Strychnos henningsii</i>	-0.32	2.34	0.25	0.58	2.00 -	6	8	37	05	06	76	30	51.35	Fine
Full	<i>Toddalopsis bremekampii</i>	-0.83	6.69	0.8649	0.779	32.021 **	5	7	223	02	03	208	1	75.68	NA
Full	<i>Tricalysia delagoensis</i>	-0.70	2.74	0.20	1.47	1.52 -	6	8	34	04	04	73	3	35.14	NA
Full	<i>Tricalysia junodii</i>	-4.00	7.64	0.87	1.12	13.61 -	2	4	159	01	04	9	0	62.16	NA
Full	<i>Uvaria caffra</i>	-1.61	4.75	0.97	0.26	120.32 **	4	6	35	03	04	43	0	32.43	NA
Full	<i>Uvaria lucida</i>	-2.45	6.91	0.95	0.57	88.10 **	5	7	197	02	04	94	3	67.57	NA
Full	<i>Vepris lanceolata</i>	-1.46	4.33	0.90	0.51	53.16 **	6	8	30	03	05	24	3	32.43	NA
Mean SCD centroid location for common species:										04	05				

Table 7: continued

Limited	<i>Balanites maughamii</i>	-0.43	1.69	0.44	0.62	7.83 *	10	12	12	07	07	18	12	13.51	Intermediate (NA)
Limited	<i>Boscia filipes</i>	0.03	0.85	0.00	0.85	0.01 -	8	10	28	06	06	52	33	48.65	Fine (NA)
Limited	<i>Brachylaena discolor</i>	-2.55	5.50	0.96	0.40	42.99 *	2	4	27	02	03	12	0	18.92	NA
Limited	<i>Burchellia bubalina</i>	-0.10	1.80	0.03	0.49	0.08 -	3	5	13	04	04	33	0	16.22	NA
Limited	<i>Combretum celastroides</i>	-0.07	1.44	0.01	0.80	0.06 -	6	8	28	05	05	67	15	43.24	Fine (NA)
Limited	<i>Erythrophleum lasianthum</i>	-0.31	1.39	0.32	0.56	4.75 -	10	12	14	08	09	3	33	29.73	Coarse (NA)
Limited	<i>Grewia microthyrsa</i>	-0.27	2.19	0.04	1.25	0.15 -	4	6	28	04	05	73	0	48.65	NA
Limited	<i>Manilkara discolor</i>	0.13	0.43	0.11	0.47	1.18 -	10	12	28	09	09	18	67	43.24	Coarse (NA)
Limited	<i>Pavetta lanceolata</i>	-1.17	3.67	0.44	1.03	2.33 -	3	5	29	03	03	67	0	35.14	NA
Limited	<i>Psidium locuples</i>	-1.21	3.78	0.79	0.69	23.03 **	6	8	23	03	05	18	3	40.54	NA
Limited	<i>Stychnos decussata</i>	0.41	-0.05	0.31	0.63	2.70 -	6	8	16	06	06	37	12	8.11	Fine (NA)
Limited	<i>Stychnos gerrardii</i>	-0.21	1.67	0.06	1.08	0.33 -	5	7	16	04	05	37	6	18.92	NA
Limited	<i>Suregada zanzibariensis</i>	-0.91	3.13	0.61	0.63	4.61 -	3	5	16	03	03	37	0	27.03	NA
Limited	<i>Tricalysia lanceolata</i>	-0.41	2.54	0.11	0.90	0.24 -	2	4	12	03	03	18	0	18.92	NA
Limited	<i>Wrightia natalensis</i>	0.31	-0.29	0.45	0.42	7.28 *	9	11	19	09	09	3	55	40.54	Coarse (NA)
Limited	<i>Zanthoxylum leprieuri</i>	-1.04	3.09	0.64	0.63	5.37 -	3	5	12	03	04	18	0	18.92	NA
										Mean SCD centroid location for common species:		05	05		

SC Size Class

\*\* Highly significant ( $p \leq 0.01$ )

\* Significant ( $p \leq 0.05$ )

- Not significant ( $p > 0.05$ )

NA Not applicable, when behind species grain, it indicates that while grain could be established, the frequency of occurrence precludes inclusion in the model



The species within the limited analysis also had some large individuals, and inverse pyramid population structures. In general, these species appeared to have shallower SCD slopes (Table 7).

A comparison of SCD slope coefficients and Y-axis intercepts of species found at both sites within the full analysis (Table 5) showed that five of the 16 species had different SCD slope coefficients or Y-axis intercepts. The important species for construction *Brachylaena huillensis* had a higher Y-axis intercept and greater density values in Tembe than in Tshanini, moreover its presence was established in nearly two thirds of the plots. However, the reverse applied for *Dialium schlechteri*, where the Tembe population had a positive slope coefficient. Only three species were comparable within the limited analyses (Table 5), and differences between sites occurred for *Balanites maughamii* with the Tembe population of this species in a better shape than its Tshanini counterpart. Only four species could be compared across analyses (Table 5) and only *Psyrdrax locuples* differed at the Y-axis intercept level.

#### *Tall Sand Forest*

This vegetation unit was newly identified in the present study (see Chapter 4), and no comparable vegetation units were established outside Tembe at that time. The main features of this unit are presented below for their own interest.

A total of 29 species were analysed in the Tall Sand Forest (Table 8). The most striking feature (full analysis) appeared in the subcanopy density of some species such as *Cola greenwayi*, *Drypetes arguta*, *Vepris lanceolata* and *Toddaliopsis bremekampii*, that exceeded 800 individuals per ha and appeared consistently in more than 80.00% of plots. While these species appeared to dominate the lower strata of this unit, *Cola greenwayi*, *Cleistanthus schlechteri* and *Dialium schlechteri* dominated the canopy level, but were found in less plots.

All species on the full analysis were classified in Type 1, while the majority of species in the limited analysis were classified in Type 3 followed by Type 1 (Table 4). *Cleistanthus schlechteri*, *Dialium schlechteri* and *Newtonia hildebrandtii* had inverse pyramid population structures, and the former and latter species had positive slope coefficients (Table 8). Mean centroid 2 was located within size class 4 for the full analysis and within size class 6 for the limited analysis. The latter clearly denotes the abundance of large trees in this vegetation unit. Mean centroid 1 was located within size classes 3 and 5 for the full and limited analyses respectively. There was no major shift between the positions of mean centroid 1 and 2 in both analyses.

Table 3: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the Tall Sand Forest in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SC range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / ha)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain	
<b>Community Level</b>	<b>Community SCD</b>	<b>-1.54</b>	<b>10.30</b>	<b>0.96</b>	<b>0.41</b>	<b>223.22</b>	<b>**</b>	<b>10</b>	<b>12</b>	<b>1038</b>						
Full	<i>Acalypha glabrata</i>	-2.80	8.14	0.96	0.46	75.01	**	3	5	88	02	03	340	0	73.33	NA
Full	<i>Cola greenwayi</i>	-1.65	7.90	0.91	0.58	69.84	**	7	9	193	04	05	1811	321	86.67	Fine
Full	<i>Croton pseudopulchellus</i>	-2.46	7.01	0.70	1.71	13.69	*	6	8	75	02	04	151	19	46.67	Fine
Full	<i>Drypetes arguta</i>	-1.52	6.96	0.74	0.88	14.44	*	5	7	97	03	04	1208	38	100.00	Fine
Full	<i>Drypetes natalensis</i>	-1.20	5.58	0.87	0.52	46.35	**	7	9	38	05	05	415	94	66.67	Fine
Full	<i>Haplocoelum foliolosum</i>	-0.98	4.63	0.38	1.53	5.42	*	9	11	47	05	06	358	132	80.00	Fine
Full	<i>Ptaeroxylon obliquum</i>	-1.01	5.34	0.83	0.54	38.71	**	8	10	45	05	07	245	226	66.67	Fine
Full	<i>Salacia leptoclada</i>	-2.22	7.21	0.92	0.47	24.30	*	2	4	51	02	03	170	0	100.00	NA
Full	<i>Toddalopsis bremekampii</i>	-1.40	6.53	0.71	0.80	9.99	*	4	6	67	03	04	811	0	93.33	NA
Full	<i>Tricalysia junodii</i>	-3.19	6.75	0.63	1.98	5.18	-	3	5	46	01	05	19	0	66.67	NA
Full	<i>Uvaria lucida</i>	-3.75	8.97	0.98	0.37	110.42	**	2	4	152	01	03	113	0	66.67	NA
Full	<i>Vepris lanceolata</i>	-1.63	7.06	0.86	0.68	37.99	**	6	8	96	03	04	1038	57	93.33	Fine
	Mean SCD centroid location for common species:										03	04				
Limited	<i>Balanites maughanii</i>	-0.47	2.39	0.16	1.39	1.85	-	10	12	12	08	09	94	75	53.33	Fine
Limited	<i>Boscia filipes</i>	0.00	1.78	0.00	1.31	0.00	-	6	8	10	05	06	113	57	53.33	Fine
Limited	<i>Cavacoa aurea</i>	-1.50	5.65	0.77	0.86	19.96	**	6	8	26	04	05	226	38	20.00	Fine (NA)
Limited	<i>Cleistanthus schlechteri</i>	0.45	0.38	0.25	0.97	3.37	-	10	12	21	08	08	113	263	40.00	Intermediate (NA)
Limited	<i>Dalbergia obovata</i>	NA	NA	NA	NA	NA	-	NA	1	13	01	NA	0	0	20.00	NA
Limited	<i>Dialium schlechteri</i>	-0.42	3.20	0.29	0.83	4.11	-	10	12	24	08	09	151	264	80.00	Intermediate
Limited	<i>Diospyros inhacaensis</i>	-0.92	4.30	0.46	1.05	5.11	-	6	8	19	05	05	264	19	60.00	Fine
Limited	<i>Dovyalis longispina</i>	-1.58	5.28	0.75	0.75	8.86	-	3	5	18	02	04	94	0	53.33	NA
Limited	<i>Euclea natalensis</i>	-2.17	5.51	0.34	2.22	1.03	-	2	4	18	02	04	57	0	60.00	NA
Limited	<i>Hymenocardia ulmoides</i>	-1.22	5.20	0.74	0.84	22.92	**	8	10	28	05	06	283	113	66.67	Fine
Limited	<i>Monodora junodii</i>	0.21	1.72	0.02	1.51	0.12	-	6	8	19	06	06	245	94	40.00	Fine (NA)
Limited	<i>Newtonia hildebrandtii</i>	0.86	-1.15	0.64	0.82	17.45	**	10	12	25	10	10	0	58	53.33	NA
Limited	<i>Pteleopsis myrtifolia</i>	-0.49	3.01	0.27	0.93	3.00	-	8	10	14	07	07	113	94	73.33	Fine
Limited	<i>Rothmannia fischerii</i>	1.17	-0.20	0.63	0.88	8.57	*	5	7	13	06	06	208	38	33.33	Fine (NA)
Limited	<i>Stychnos decussata</i>	0.23	1.15	0.03	1.45	0.26	-	8	10	18	06	06	189	151	80.00	Fine
Limited	<i>Stychnos henningsii</i>	-0.31	3.64	0.16	0.75	1.14	-	6	8	29	05	05	434	75	100.00	Fine
Limited	<i>Tricalysia delagoensis</i>	0.65	1.63	0.07	1.88	0.24	-	3	5	11	03	04	113	0	26.67	NA
	Mean SCD centroid location for common species:										05	06				
SC	Size Class															
**	Highly significant ( $p \leq 0.01$ )															
*	Significant ( $p \leq 0.05$ )															
-	Not significant ( $p > 0.05$ )															
NA	Not applicable, when behind species grain, it indicates that while grain could be established, the frequency of occurrence precludes inclusion in the model															



### *Afzelia quanzensis* unit

The *Afzelia quanzensis* unit is also a new vegetation unit established during the present study. While *Afzelia quanzensis* was the characteristic species usually forming the canopy of this vegetation unit, was not the most abundant species. The subcanopy was dominated by a stand of *Vepris lanceolata* (Table 9). Mean centroid 1 was located within size class 3 for both analyses and mean centroid 2 within size class 7 for the full analysis and within size class 5 for the limited analysis. There was a major shift between the positions of mean centroid 1 and 2 in the full analysis (four size classes changes), and a shift of two size classes in the limited analysis.

Results of the limited analysis showed that the subcanopy level was shared by *Diospyros inhacaensis*, *Drypetes arguta*, *Drypetes natalensis* and *Euclea natalensis*. The canopy level was shared by *Vepris lanceolata* and *Dialium schlechteri* with some emergents from *Cola greenwayi* and *Diospyros inhacaensis*. In general, this community was of a fairly low stature, reaching heights of 8 to 10 m for the larger trees.

The two species in the full analysis belonged to Type 1, and so did most species in the limited analysis, although there were two species in Type 3 (*Ochna barbosae* and *Dialium schlechteri*).

### *Grain of species and communities*

The grain of species was noted for all species for which it was possible to identify grain by using the general model presented in Figure 1. The graphical identification of grain appears in Figures 2 – 11 for the various vegetation units (compare Tables 2, 3, 6, 7, 8 and 9). Most species were fine-grained (Table 10), and therefore all vegetation units sampled here were considered fine-grained (Table 10). The Sand Forest Association in general was a fine-grained forest. Interestingly, the species classified as coarse or intermediate-grained were usually those that grow into large canopy trees such as the canopy trees that define the Sand Forest (*Newtonia hildebrandtii*, *Cleistanthus schlechteri*, *Balanites maughamii*, *Erythrophleum lasianthum* and *Dialium schlechteri*). However, they represented the minority in terms of the number of species classified.

In general, there were more species with a fine-grain character in Tshanini than in Tembe. However, the Tall Sand Forest in Tembe had a definitive fine-grain character and had the most species classified.

Table 9: Detail of species level size class distribution (SCD) regressions, including statistical significance, the range of size classes (SC) used, number of individuals sampled, centroid 1 position (full data set) centroid 2 position (size classes 3 - 12), subcanopy and canopy density, frequency of occurrence in sample plots, and species grain. The information presented is for the common species for which 30 or more individuals were sampled (full analysis) and those for which 10 to 29 individuals were sampled (limited analysis) of the *Afzelia quanzensis* clumps vegetation unit in Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa

Analysis	Species	Slope	Intercept	R <sup>2</sup>	Standard error	F	Degrees of freedom	SC range	Number of individuals	Centroid 1 in SC	Centroid 2 in SC	Subcanopy density (individuals / ha)	Canopy density (individuals / ha)	Frequency of occurrence (%)	Species grain	
<b>Community Level</b>	<b>Community SCD</b>	<b>-1.64</b>	<b>8.54</b>	<b>0.88</b>	<b>0.77</b>	<b>71.50</b>	<b>**</b>	<b>10</b>	<b>12</b>	<b>297</b>						
Full	<i>Haplocoelum foliolosum</i>	-1.34	4.33	0.32	2.27	3.82	-	8	10	31	02	08	50	50	66.67	Fine
Full	<i>Vepris lanceolata</i>	-1.50	7.49	0.87	0.62	39.22	**	6	8	31	04	05	1100	250	100.00	Fine
Mean SCD centroid location for common species:											03	07				
Limited	<i>Cola greenwayi</i>	-0.92	7.38	0.12	2.59	0.83	-	6	8	12	03	05	100	50	66.67	Fine
Limited	<i>Dialium schlechteri</i>	0.03	0.07	0.00	1.75	0.00	-	9	11	10	07	08	167	333	66.67	Intermediate
Limited	<i>Diospyros inhacaensis</i>	-1.92	13	0.76	1.14	18.98	**	6	8	19	03	05	450	50	66.67	Fine
Limited	<i>Drypetes arguta</i>	-2.07	54	0.77	0.91	10.31	*	3	5	28	02	04	450	0	66.67	NA
Limited	<i>Drypetes natalensis</i>	-0.72	34	0.10	2.07	0.58	-	5	7	15	03	05	350	0	33.33	NA
Limited	<i>Euclea natalensis</i>	-2.03	65	0.90	0.65	46.88	**	5	7	26	02	05	350	0	66.67	NA
Limited	<i>Monanthes caffra</i>	NA	NA	NA	NA	NA	NA	1	11	11	01	NA	0	0	33.33	NA
Limited	<i>Ochna barbosae</i>	4.95	-0.48	0.44	3.91	0.77	-	1	3	11	02	03	222	0	66.67	NA
Limited	<i>Toddalopsis bremekampii</i>	-1.47	6.77	0.72	0.67	5.12	-	2	4	14	02	03	300	0	66.67	NA
Mean SCD centroid location for common species:											03	05				

SC Size Class

\*\* Highly significant (p ≤ 0.01)

\* Significant (p ≤ 0.05)

- Not significant (p > 0.05)

NA Not applicable, when behind species grain, it indicates that while grain could be established, the frequency of occurrence precludes inclusion in the model



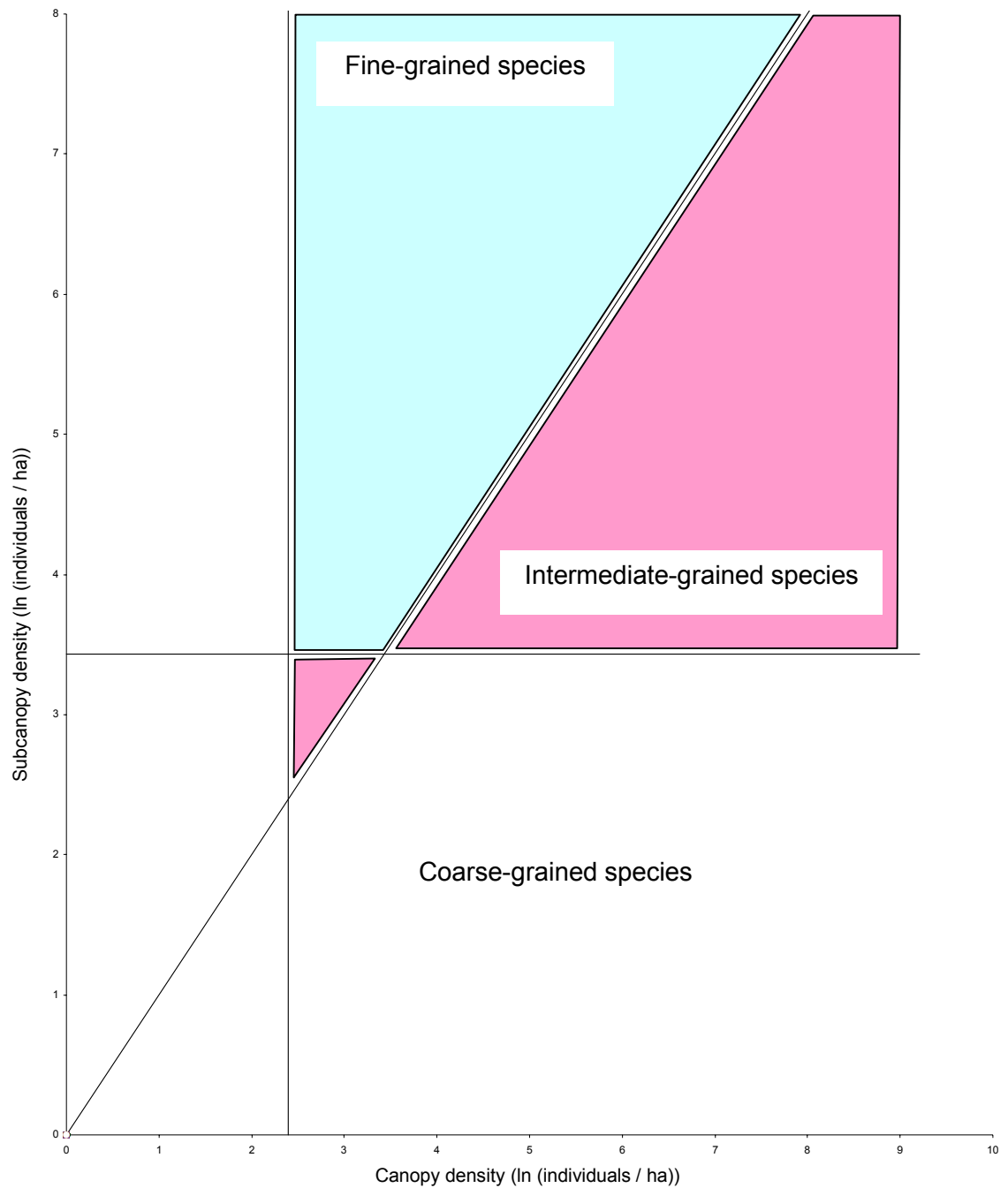


Figure 1: The graphical grain determination model based on canopy density (X-axis) and subcanopy density (Y-axis) used to evaluate tree species grain in the two study sites in KwaZulu-Natal, South Africa. Values are ln-transformed to improve readability. The model is adapted from Lawes and Obiri (2003).

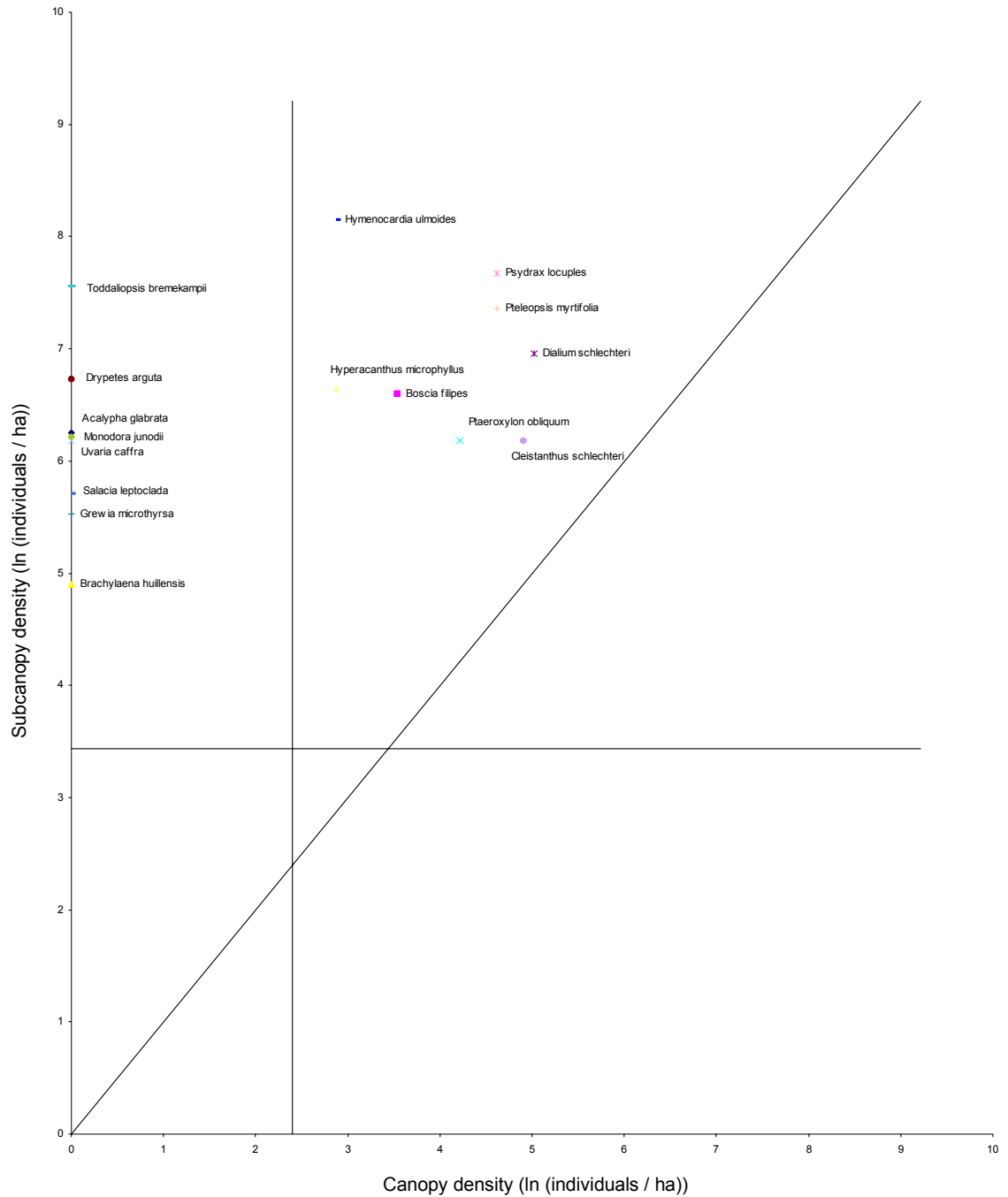


Figure 2: The grain of Short Sand Forest woody species for which at least 30 individuals were sampled in Tshanini Community Conservation Area, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

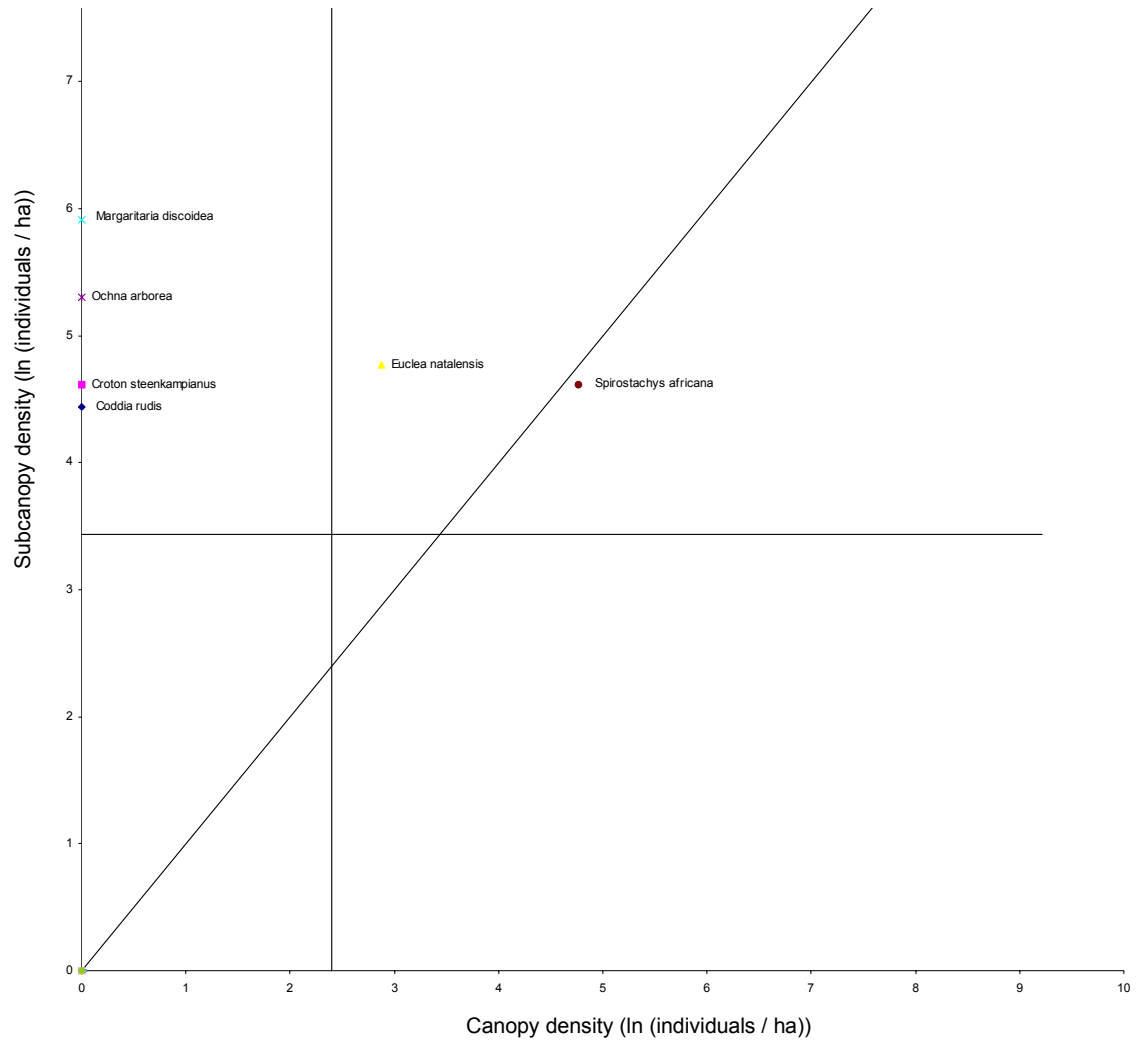


Figure 3: The grain of Short Sand Forest woody species for which 10 to 29 individuals were sampled in Tshanini Community Conservation Area, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

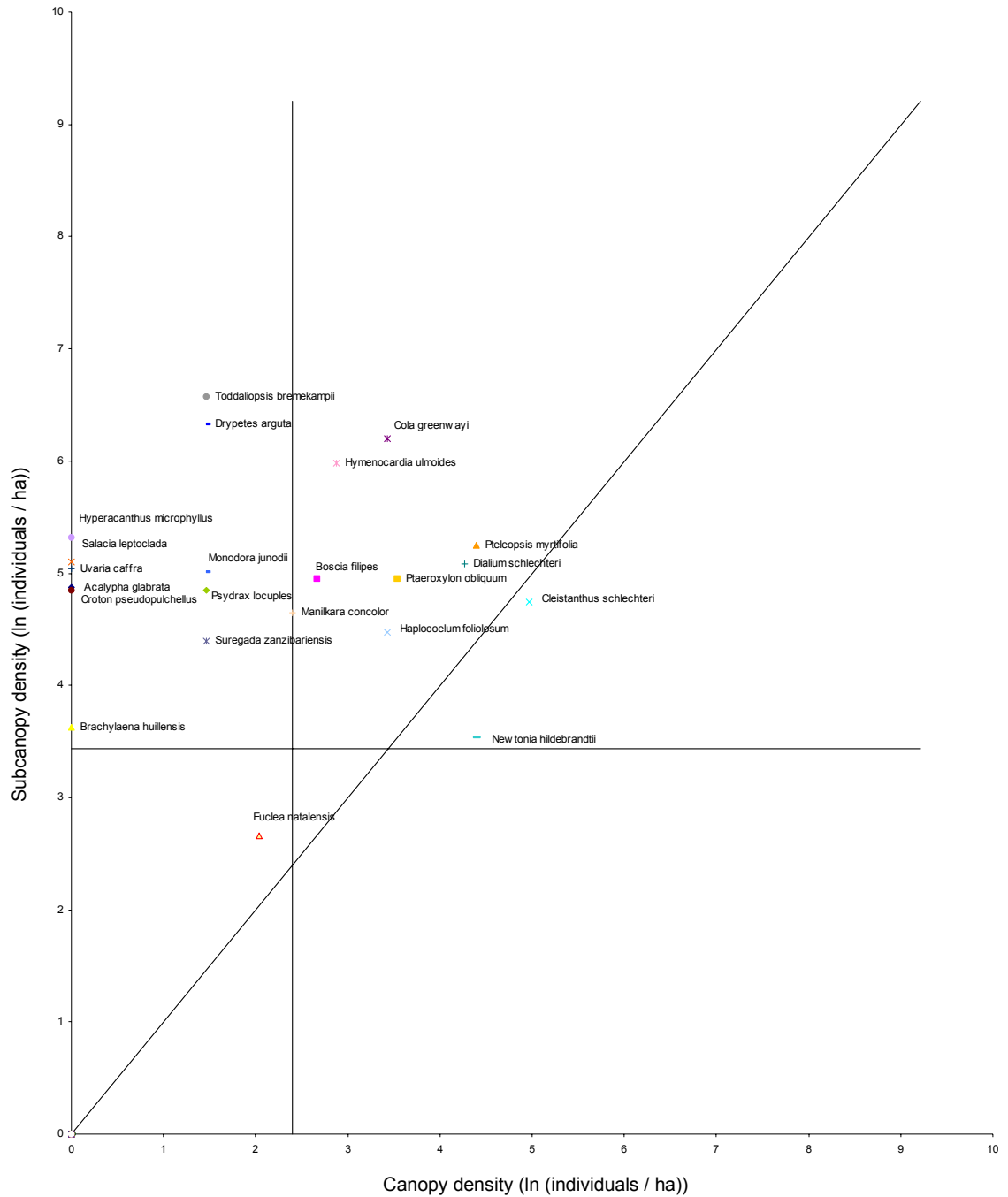


Figure 4: The grain of Intermediate Sand Forest woody species for which at least 30 individuals were sampled in Tshanini Community Conservation Area, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

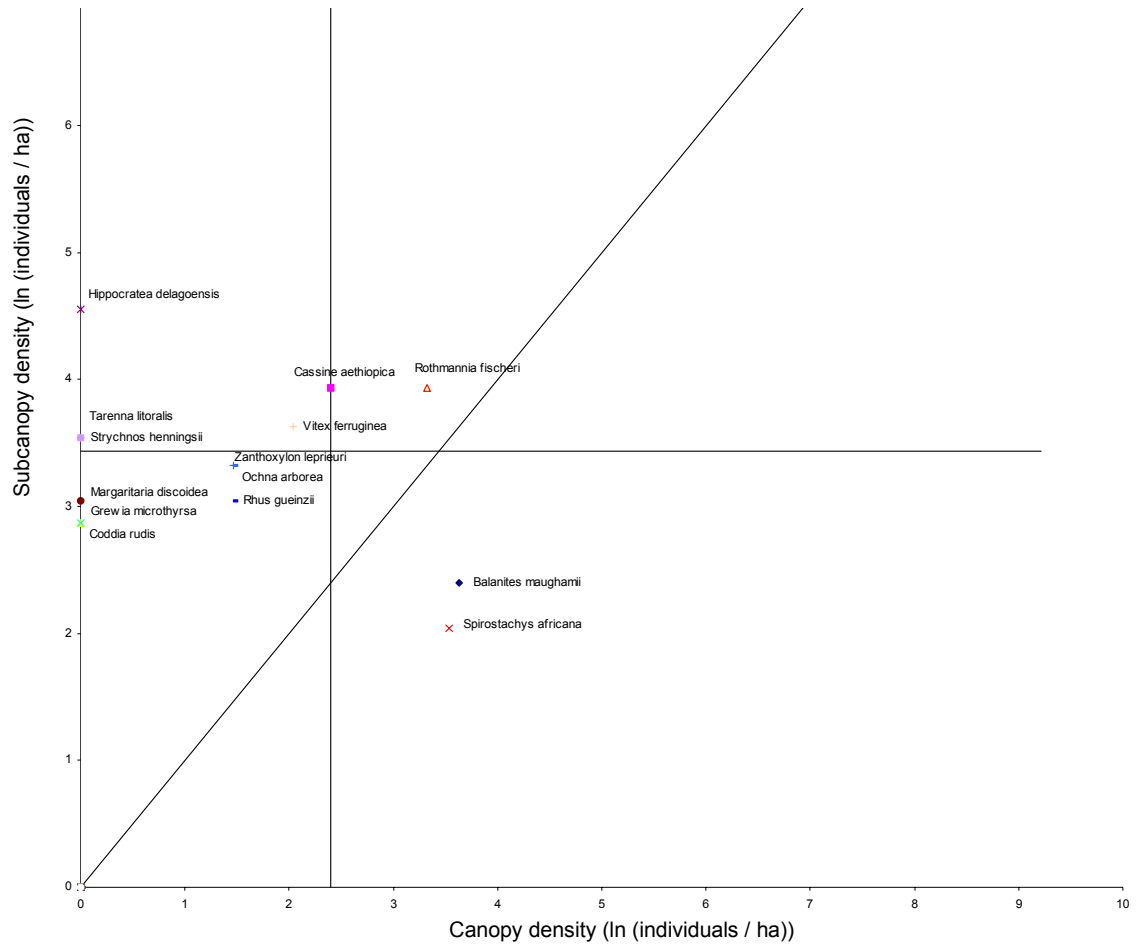


Figure 5: The grain of Intermediate Sand Forest woody species for which 10 to 29 individuals were sampled in Tshanini Community Conservation Area, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

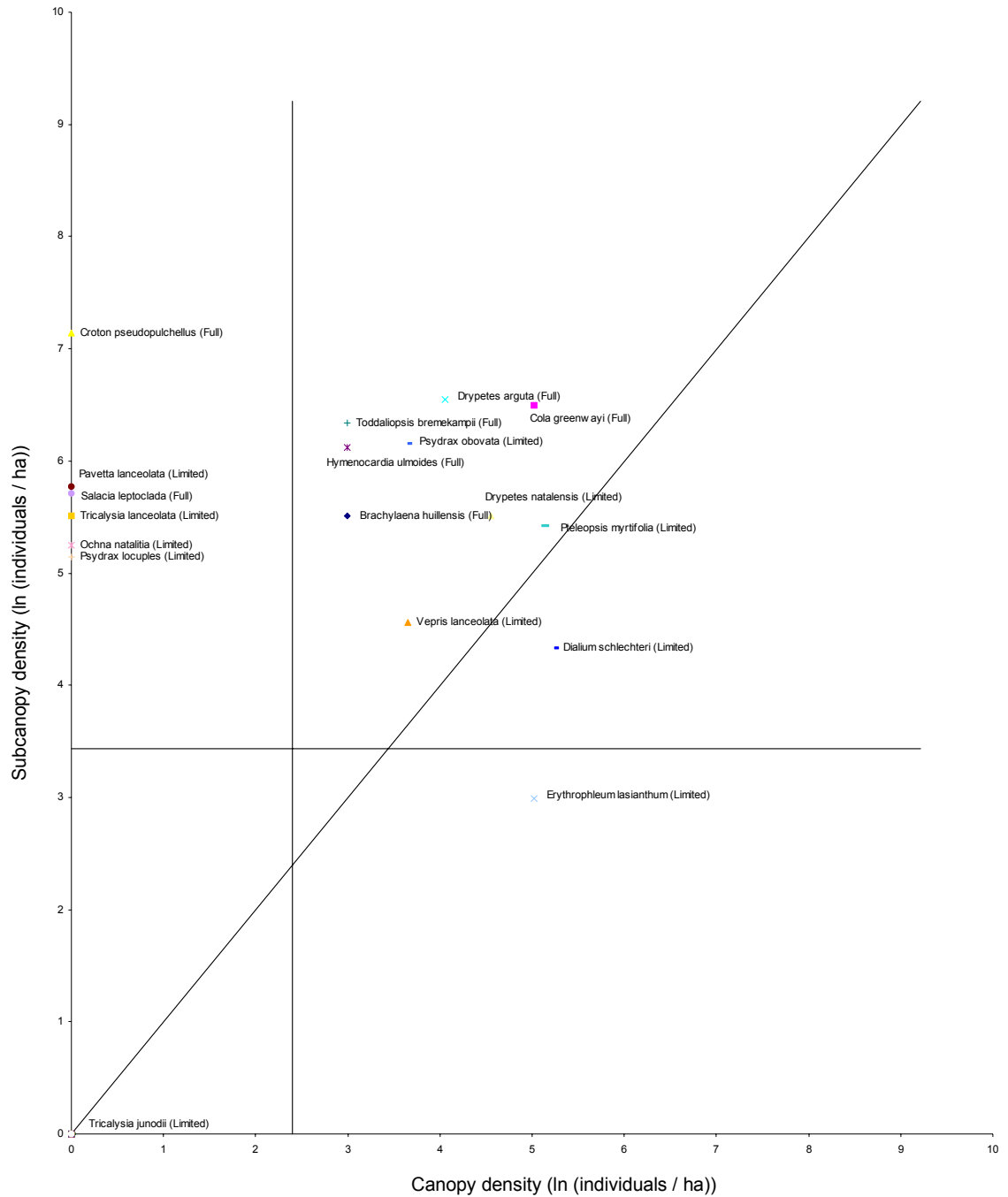


Figure 6: The grain of Short Sand Forest woody species sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability. The full analysis represents species for which at least 30 individuals were sampled, while the limited analysis represents species for which only 10 to 29 individuals were sampled.

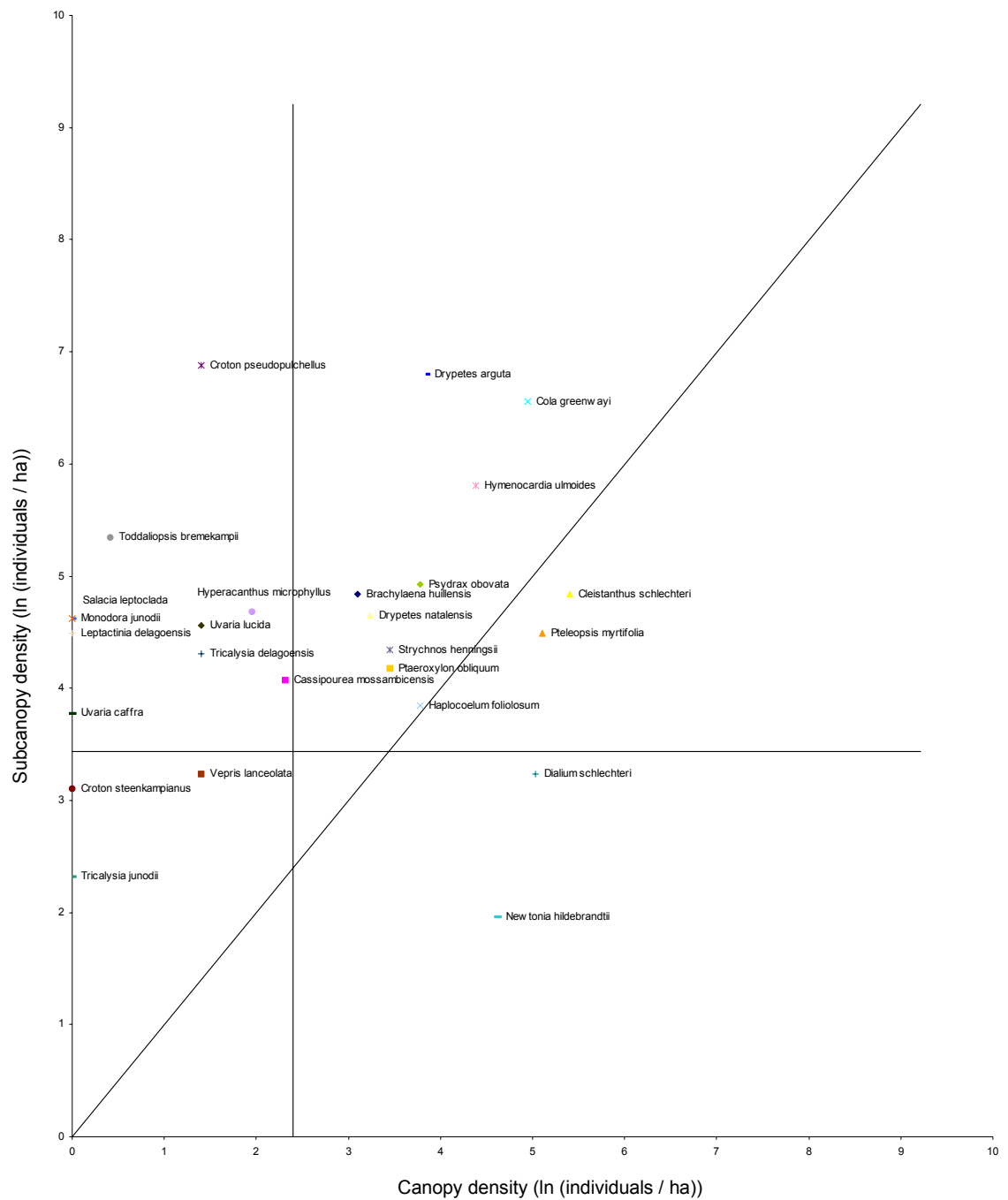


Figure 7: The grain of Intermediate Sand Forest woody species for which at least 30 individuals were sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.



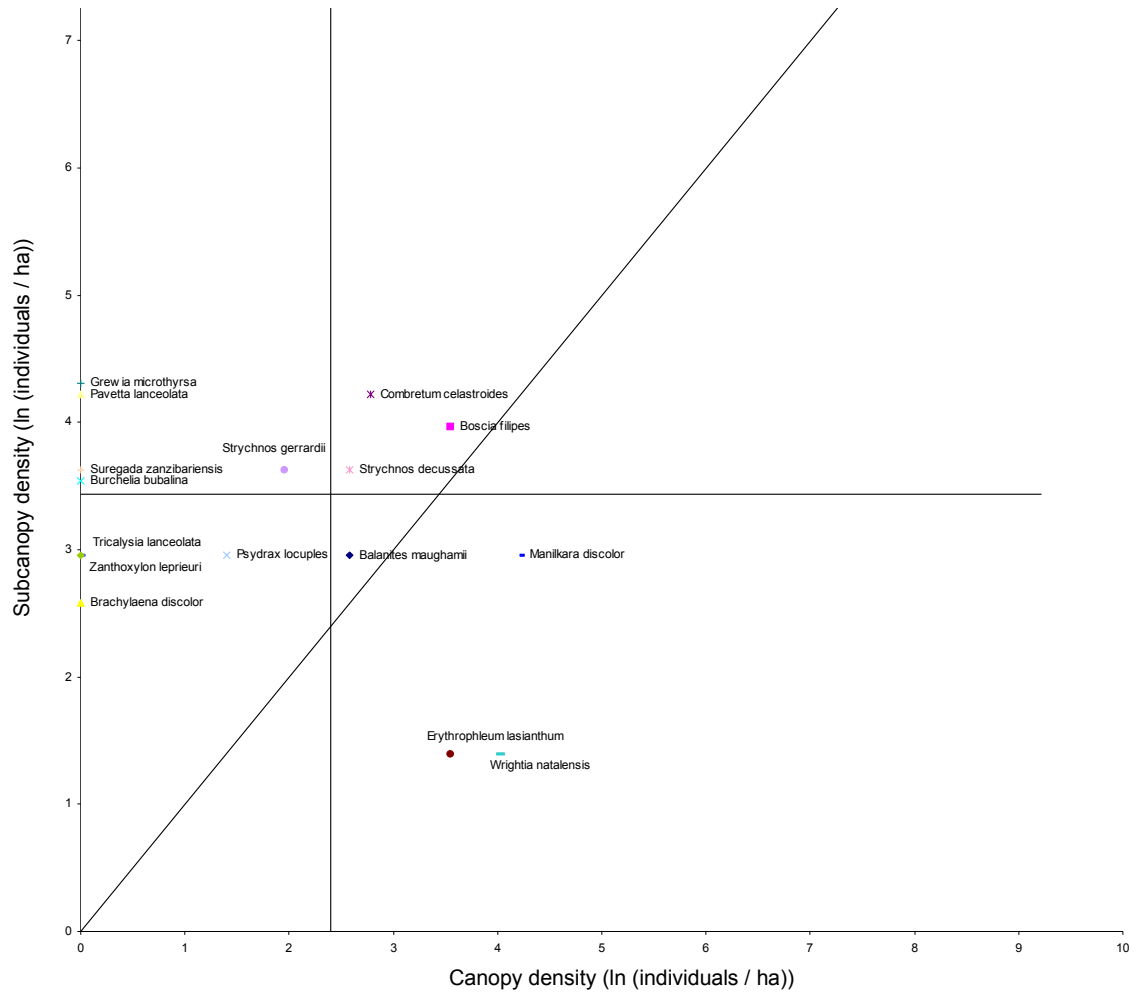


Figure 8: The grain of Intermediate Sand Forest tree species for which 10 to 29 individuals were sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

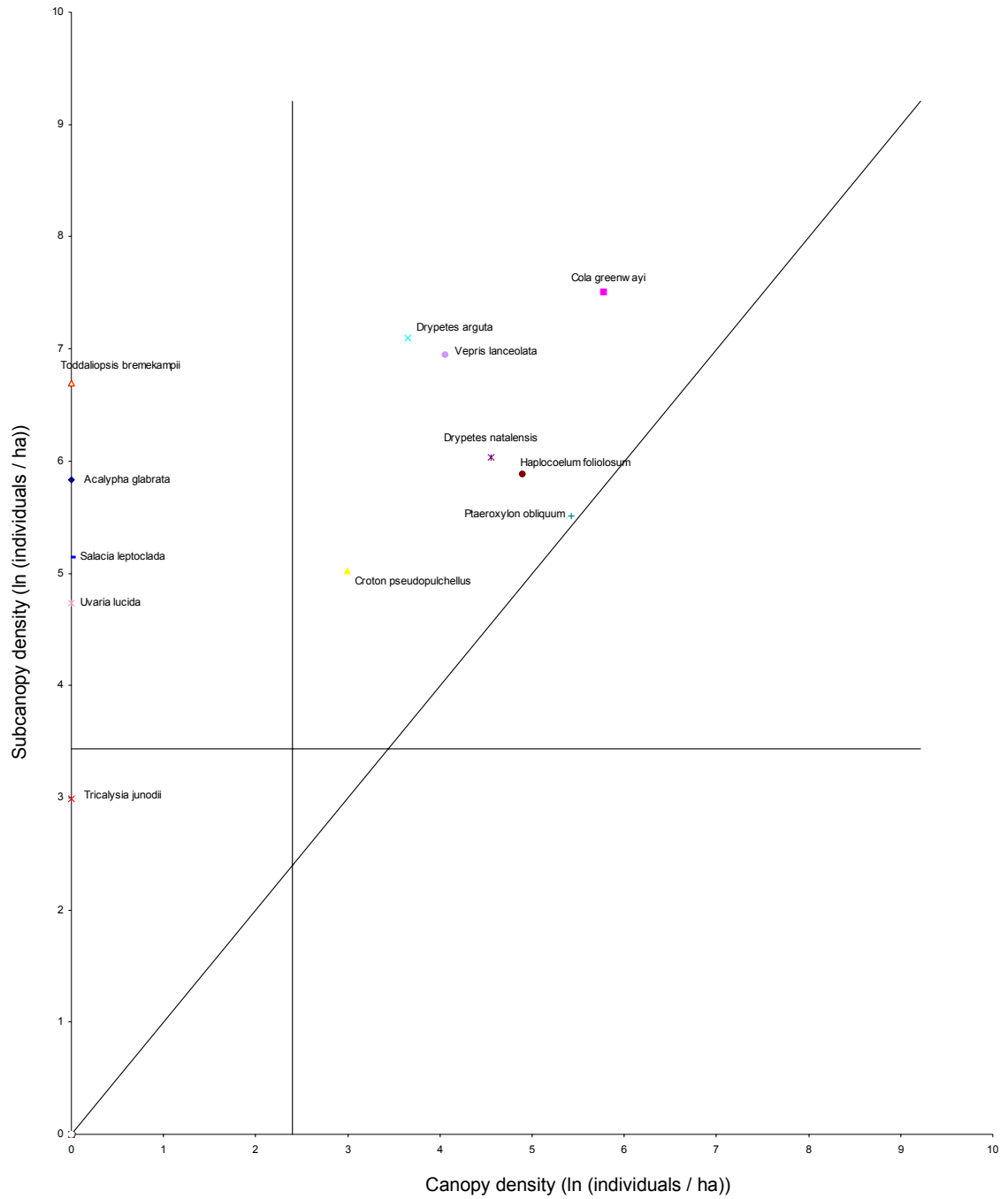


Figure 9: The grain of Tall Sand Forest woody species for which at least 30 individuals were sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

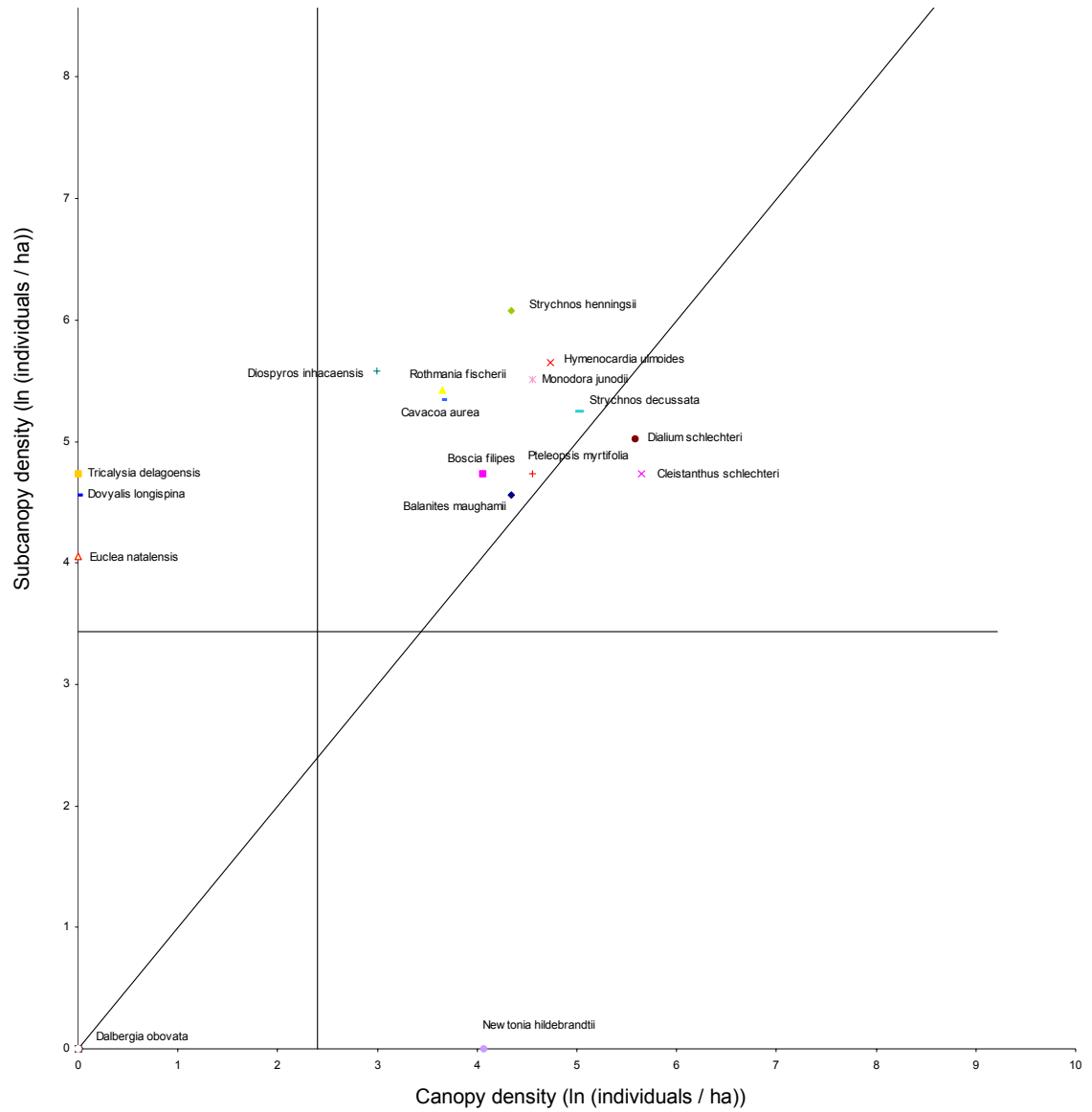


Figure 10: The grain of Tall Sand Forest woody species for which 10 to 29 individuals were sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability.

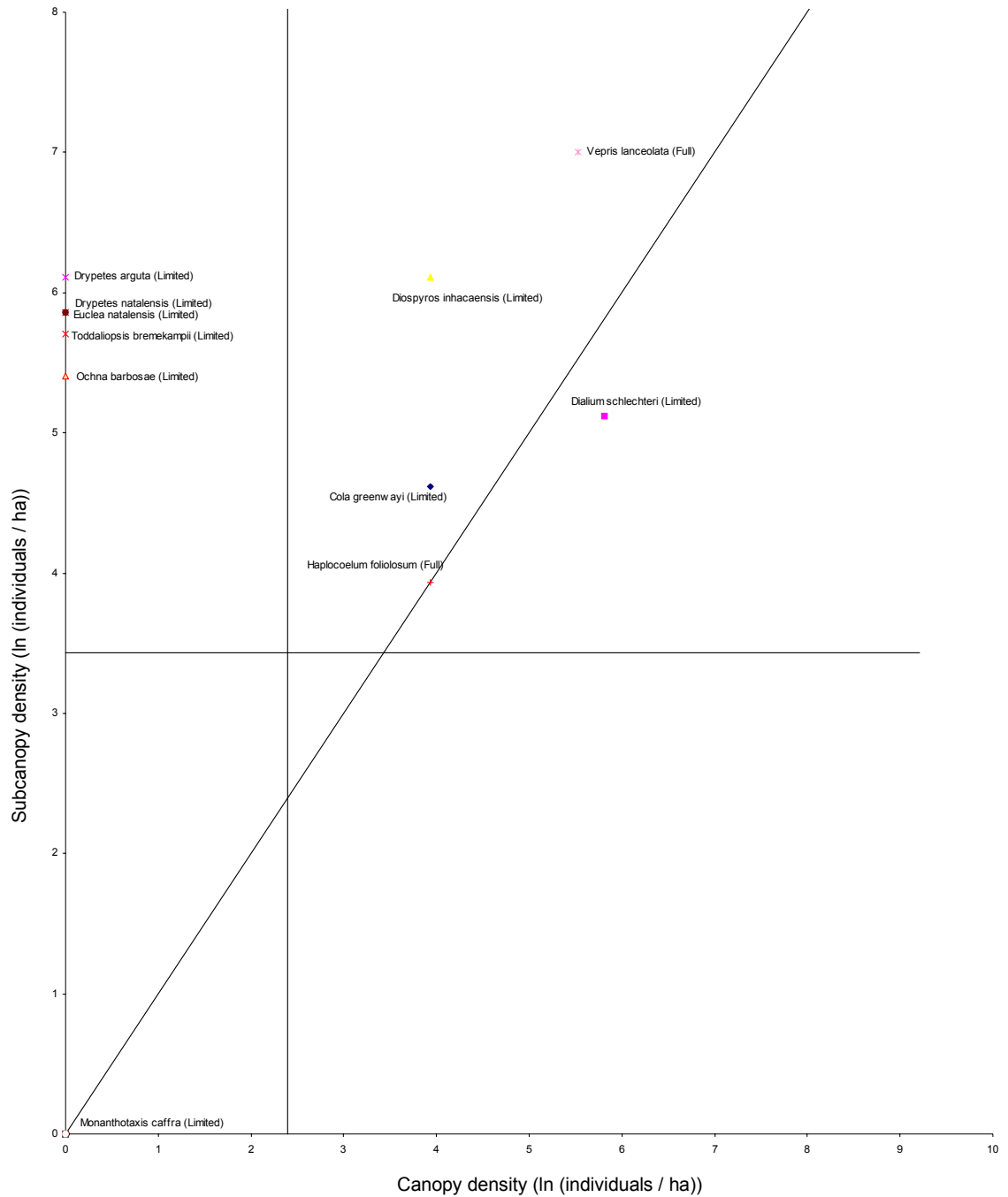


Figure 11: The grain of *Azelia quanzensis* clumps community woody species sampled in Tembe Elephant Park, KwaZulu-Natal, South Africa. Values have been ln-transformed to improve readability. The full analysis represents species for which at least 30 individuals were sampled, while the limited analysis represents species for which only 10 to 29 individuals were sampled.

Table 10: The number of species by grain category and the derived community grain for the various vegetation units of Tshanini Community Conservation Area (TCCA) and Tembe Elephant Park (TEP), Maputaland, northern KwaZulu-Natal, South Africa

Grain	Number of species per grain category by vegetation units and sites					
	Short Sand Forest		Intermediate Sand Forest		Tall Sand Forest	<i>Azelia quanzensis</i> clumps
	TCCA	TEP	TCCA	TEP	TEP	TEP
<b>Fine</b>	7	6	9	7	14	4
<b>Intermediate</b>	1	1	2	2	1	1
<b>Coarse</b>	0	1	1	2	0	0
	Derived status of the vegetation unit or sub-unit					
<b>Fine</b>	X	X	X	X	X	X
<b>Intermediate</b>	-	-	-	-	-	-
<b>Coarse</b>	-	-	-	-	-	-



## Discussion

The general perception from the present study was that there was a remarkable similarity between the two sites at most levels. From the species that could be compared, 50.00% had similar SCD structures in the Short Sand Forest, while 69.56% of species had similar SCD structures in the Intermediate Sand Forest. Both sites appeared to have a majority of their most common species populations (full analysis, Table 4) classified within Type 1, representing self-sustaining populations (Everard *et al.* 1994; Lykke 1998; Niklas *et al.* 2003). The less abundant species (limited analysis, Table 4) were generally found more within Type 3, which represents flat or positive slopes, indicating potentially declining populations (Lykke 1998) or mature long-lived early successional species that have survived up to the present (Condit *et al.* 1998). Looking at a combined value for both analyses (Table 4), it was clear that Type 1 dominated in nearly all sites, while Type 2 was equally important in the Intermediate Sand Forest of Tshanini.

Moreover, in both analyses the centroids were generally skewed to the left of the size class distributions, which confirmed that these populations had good regenerative potential (Niklas *et al.* 2003), further confirmed by mostly pyramidal population structures. A similarity between sites at the phytosociological level was already highlighted by (Gaugris *et al.* 2004), and the present study confirmed this similarity.

Differences in abundance between the two sites were observed in three common species, *Drypetes arguta*, *Dialium schlechteri* and *Pteleopsis myrtifolia*, in the Short Sand Forest, while *Toddaliopsis bremekampii* and *Hymenocardia ulmoides* were similar. The differences in the Short Sand Forest indicate that common species populations in Tshanini are in better condition than in Tembe. In the Intermediate Sand Forest, differences were observed within five common species while the other five shared species were similar. In the Intermediate Sand Forest, *Cola greenwayi* and *Croton pseudopulchellus* had steeper slopes and higher Y-axis intercepts in Tembe than in Tshanini, denoting healthier populations (Lykke 1998; Niklas *et al.* 2003; Boudreau *et al.* 2005) although the Tshanini populations were not declining. However, the other three common species found to be different were in better shape in Tshanini than in Tembe, especially in the case of *Dialium schlechteri* where the population in Tembe showed a positive slope coefficient. While these differences are weak, it appears that common species have begun to show differences and that populations in Tshanini appear closer to the ideal population structure defined by a range of authors



(Everard *et al.* 1994; Everard *et al.* 1995; Peters 1996; Niklas *et al.* 2003) than in Tembe.

An interesting case was that of *Brachylaena huillensis*, which was a relatively abundant species at both canopy and subcanopy levels in the Intermediate Sand Forest of Tembe (Table 7), but rare (frequency < 10.00%) and only found at the subcanopy level in Tshanini (Table 6). This is the most highly sought after species for building construction by local people (Gaugris *et al.* 2007), and its abundance in Tshanini is suspiciously low. Selective extraction of this species in the past appears a relatively credible option to explain its low abundance and its absence from the canopy level.

It is not always possible to pinpoint a particular reason for differences at the species level. Variations could be linked to natural variations in the forest, without a particular influence from either man or herbivores (Chapman *et al.* 1997; Burslem and Whitmore 1999; Chapman *et al.* 1999), but also to either of these elements separately or their absence altogether (Chapman and Chapman 1997; Babaasa 2000; Maisels *et al.* 2001; Mosugelo *et al.* 2002; Babaasa *et al.* 2004; Western and Maitumo 2004; Boudreau *et al.* 2005; Banda *et al.* 2006; Botes *et al.* 2006; Western In Press), as Tembe is influenced by animals and not by people, while Tshanini has not been influenced by either since 1992 (Gaugris 2004).

Fire, although a noteworthy agent in Africa (Bond *et al.* 2003; Bond and Keeley 2005; Bond *et al.* 2005) appears an unlikely candidate here as Sand Forest in both sites has not burned in a significant manner recently (Gaugris 2004; Matthews 2006), and the small burned patches currently appear to be regenerating as woodlands (Matthews 2006), and were therefore not included in this sample. The close proximity of the two sites in space also most likely rules out climatic factors particular to one site as an explanation to these differences (Yeh *et al.* 2000). Additionally, no disturbance of climatic or catastrophic nature as defined by Whitmore and Burslem 1996, or Burslem and Whitmore (1999), has been recorded since 1989, or even 1983 (Matthews 2006; Guldmond 2006), and therefore the most likely answer lies in the influence of herbivores and man.

The fact that people and fire are eliminated from Tembe as disturbance agents indicates that the differences observed between the two sites are potentially attributable to an influence from herbivores. However, at this stage it appears equally possible that the lack of any disturbance agent in Tshanini could explain these differences. A similar situation was observed in Cameroon by Maisels *et al.* (2001). Woody species in Tshanini are more evenly spread between Types 1 and 2 than in



Tembe. Type 2 species have less steep distributions, but are not flat, and are defined as species with shrinking populations in the sense that the regeneration pool is diminished (Condit *et al.* 1998; Niklas *et al.* 2003). As canopies close in mature forests, the abundance of smaller trees becomes lower as the light continuum in the subcanopy decreases (Poorter *et al.* 1996; Babaasa *et al.* 2004), but when gaps are opened, the abundance of such small classes usually increases (Babaasa *et al.* 2004). The size of gaps is influential, as the regeneration of Type 1 species occurs mainly in minor gaps such as branch breaks but Type 3 species need substantially larger gaps (Everard *et al.* 1994; Everard *et al.* 1995).

Because Type 3 species in Tembe and Tshanini show relatively poor regeneration with inverse pyramidal structures, and because the abundance of Type 3 species was more or less similar at both sites (Table 4), the hypothesis that these species are long-lived early successional species that persist in the canopy level and regenerate irregularly (Everard *et al.* 1994; Everard *et al.* 1995; Poorter *et al.* 1996; Burslem and Whitmore 1999) appears most likely. If the hypothesis holds true, then sampling in the present study did not encounter signs of large Type 3 favourable gaps, which concurs with the author's personal observations. The spread of Type 1 and 2 species is therefore interesting in the sense that it could represent the presence of small Type 1 favourable gaps in Tembe, whereas they are less frequent in Tshanini. Again personal observation concurs with this option, and no gaps were sampled in Tshanini, whereas gaps were represented in the sampling in Tembe. It is however important to note that Type 1 species can also regenerate without gaps or otherwise in transient gaps, such as quickly replaced broken branches (Burslem and Whitmore 1999), it appears therefore also possible that some gaps may not have been obviously noticeable during the sampling. Canopy gaps in the Sand Forest of Tembe have been described as elephant refuges of two sizes (Shannon 2001). A grade 2 refuge represents a small opening of the canopy, but a grade 1 refuge represents large clearings of 20 m diameter and larger. Both refuges represent what is commonly known as gaps, and it appears likely that both refuge types will contribute to an increased level of direct light penetration to the subcanopy level (grade 1 refuge), or an improved light continuum throughout the subcanopy level (grade 2 refuge). The hypothesis that elephants are creating gaps in the Sand Forest could contribute to the greater proportion of tree species classified in Type 1 in Tembe.

While differences are difficult to explain, a tentative account of Sand Forest structure and dynamics appears possible. The Short Sand Forest is defined as a dense thicket-like vegetation of short stature, rarely exceeding 8 m in height (Matthews *et al.*





2001; Izidine *et al.* 2003; Gaugris and Van Rooyen In Press) or 10 m as defined in the present study (see chapter 4). In the present study it is shown that the subcanopy density often exceeds 800 individuals per hectare for a range of medium to large sized woody species that appear to be in a short form in this particular unit. These species are *Croton pseudopulchellus*, *Dialium schlechteri*, *Drypetes arguta*, *Hymenocardia ulmoides*, *Psydrax locuples*, *Pteleopsis myrtifolia* and *Toddaliopsis bremekampii*. The upper canopy is dominated by some of these species, although at a much lower density than the subcanopy level, and apart from *Cleistanthus schlechteri* and *Dialium schlechteri*, which emerge above the uniformly low canopy, there are no other real large canopy trees. Nearly all species have pyramidal population structures whereby the subcanopy density is greater than the canopy density, and some woodland species, such as *Spirostachys africana*, occur in the canopy. The centroid location skewed to the left indicates a young and dynamic subcommunity (Niklas *et al.* 2003), while the size class range rarely exceeds size class 9, indicating that not many trees have reached their potential stem diameter. The lack of major shift in size classes between the locations of centroids 1 and 2 indicates that small individuals do not contribute disproportionately to the observed size class distributions.

The Intermediate Sand Forest, previously described as Tall Sand Forest (Matthews *et al.* 2001; Gaugris *et al.* 2004; Gaugris and Van Rooyen In Press), has been reclassified as Intermediate Sand Forest as it appears to form a link between the Short Sand Forest and a new unit called Tall Sand Forest in this study. The subcanopy density rarely exceeds 400 individuals per hectare for any species, and the bulk of species have densities within the 100 to 300 individuals per hectare. This unit has the highest species count and reaches heights of 12 m with emergents around 15 m (see Matthews *et al.* 2001, Gaugris *et al.* 2004, Gaugris and Van Rooyen in press). The size class range is complete, with many species found in the large to very large size classes (size classes 10 to 12). Interestingly, some of these large trees are also the emergents from the Short Sand Forest, such as *Dialium schlechteri*, *Hymenocardia ulmoides*, *Psydrax locuples*, *Pteleopsis myrtifolia* and *Toddaliopsis bremekampii*, and new species have appeared in the canopy, such as *Brachylaena huillensis*, *Cola greenwayi*, *Newtonia hildebrandtii* and *Ptaeroxylon obliquum*. The centroid location is closer to the middle of the size class distribution, thus indicating the presence of large and mature trees, but still an abundance of smaller trees.

The Tall Sand Forest described in the present study (see Chapter 4) shows another picture altogether. The unit has a tall tree stratum of 12 to 15 m and a second lower canopy at 10 m. In terms of density this unit is characterised by the



reappearance of subcanopy densities in excess of 1000 individuals per ha for some species (*Cola greenwayi*, *Drypetes arguta*, *Vepris lanceolata*), while larger trees such as *Cleistanthus schlechteri*, *Dialium schlechteri*, *Newtonia hildebrandtii* and *Ptaeroxylon obliquum* dominate the canopy. The centroid position of species encountered the most shows a blatant skew to the left, while the centroid position of species encountered least often shows a centroid located in the middle of the size class distribution, thus indicating the most mature stage encountered as yet. Individuals in the large to very large size classes in the latter group are commonplace. The shift observed between mean centroid positions shows that the species found most often are influenced by seedlings and saplings, indicating potentially good recruitment (Niklas *et al.* 2003), while the species found least often, have problematic size class distributions as evidenced by a number of flat or shallow slope coefficients.

The descriptions above illustrate clear distinctions in the Sand Forest structure, with the presence of various layers at different heights, as well as a wealth of species groups in different successional stages. Additionally, the Short and Intermediate Sand Forest were found to potentially harbour a greater number of species (Pers. Obs.: although this is an impression rather than a demonstrated fact, due to unequal sample sizes between the vegetation units) than the Tall Sand Forest, thereby potentially indicating a more mature forest stage for the last subcommunity (Burslem and Whitmore 1999). This diversity observed in Sand Forest bears similarities to a hypothesis of Burslem and Whitmore (1999) describing what could be a successional transition from Short to Tall Sand Forest: a suite of species appears in the Short Sand Forest and is maintained in the Intermediate Sand Forest stage. The Intermediate Sand Forest stage leads to the establishment of a tall (12 – 15 m) canopy of large trees (Tall Sand Forest), while the undergrowth goes through another change as light conditions are modified once this tall canopy has emerged.

The species level comparisons portray a relatively different picture than the vegetation unit level comparisons presented in the previous chapter. As such the comparable species of the Short and Intermediate Sand Forest are mostly similar in terms of slope and Y-axis intercepts, but the unit level comparisons displayed significant differences between the comparable Sand Forest units of the two sites. However, in the present part of the study, relatively few of the species that were analysed could be compared. Only eight species (24.24%) were comparable from a total of 33 species analysed for the Short Sand Forest across both sites, and 23 species (42.81%) compared from a total of 55 species analysed across both sites for the Intermediate Sand Forest. This remarkable similarity at the comparable species



level should be interpreted with caution as the majority of common species could not be compared between the two sites. It appears most likely that differences at the unit level must be linked to these other species. The implications of this difference are far reaching, as it appears that common species of the two sites now exhibit such differences in abundance that they can no longer be compared. Although there is no statistical comparison presented, the impossibility to compare such species between the two sites attests the difference at the common species level.

The concept of grain originates from forestry ecology in South Africa (Midgley *et al.* 1990; Everard *et al.* 1994; Everard *et al.* 1995), and represents a spatial analysis comparing number of individuals of a species at the subcanopy and canopy levels (Everard *et al.* 1994; Everard *et al.* 1995; Obiri *et al.* 2002; Lawes and Obiri 2003). The grain of a species indicates the scale of regeneration of the species. Coarse-grained species have relatively few individuals in the subcanopy level compared to the canopy level, while the reverse holds true for fine-grained species (Obiri *et al.* 2002; Lawes and Obiri 2003). Coarse-grained species are believed to regenerate over large areas at low densities, and may not withstand intense utilisation. Fine-grained species have well-balanced subcanopy and canopy levels that reflect a typical inverse J-shaped distribution, which is considered the ideal population structure (Obiri *et al.* 2002; Lawes and Obiri 2003).

The grain of species and communities established in the present study must be evaluated in conjunction with the classification into Types (Everard *et al.* 1994; Everard *et al.* 1995; Obiri *et al.* 2002). A wealth of Type 1 species and an abundance of the same species at both subcanopy and canopy levels define fine-grained forests (Everard *et al.* 1994; Everard *et al.* 1995). As such it is therefore fairly conclusive that Sand Forests are fine-grained forests (Tables 4 and 10).

A definition of fine-grained forests is needed before developing the Sand Forest case further. Fine-grained forests are defined as populated by shade-tolerant fine-grained species, where the scale of variation from patch to patch is small (Midgley *et al.* 1990; Everard *et al.* 1994; Everard *et al.* 1995). The scale of variation in the concept of grain applies to “the scale at which normal dynamic regeneration processes occur” (Everard *et al.* 1995) while patch is loosely used to define structures that range from a few acres to hundreds of hectares or more. Based on such assumptions, it appears possible that small patches of forest can exist as sustainable entities (Everard *et al.* 1995). Moreover, a small scale of variation means that small gaps are sufficient to ensure successful regeneration of species. However, the grain of a forest concept does not include other processes that contribute to regeneration, such as pollination and



seed dispersal, which are thought to function at a different scale altogether (Everard *et al.* 1995; Maisels *et al.* 2001; Babweteera *et al.* 2007; O'Connor *et al.* 2007).

In terms of dynamics, the fine-grain pattern indicates that at the patch level, even small, Sand Forest is likely to sustain and regenerate itself. However, the diversity observed in avian species assemblages (Van Rensburg *et al.* 2000) and the indications from dung beetles used as indicators of forest condition and disturbance (Van Rensburg *et al.* 1999; McGeogh *et al.* 2002; Botes *et al.* 2006) suggest that diversity between patches is such that many patches over a large area are required to conserve the dynamics of Sand Forest in general, and that these forests are susceptible to over-utilisation by man and elephants. The present study supports the notion that elephants are important agents affecting Sand Forests dynamics through the creation of small gaps and associated changes in the light continuum. However, in a small and confined reserve where elephant populations increase in numbers (Morley 2005; Guldmond 2006), the risk that elephants will open larger gaps increases (O'Connor *et al.* 2007). Large gaps are most likely to provoke a change in the forest dynamics or a successional change to woodlands altogether (Van Rensburg *et al.* 1999; Van Rensburg *et al.* 2000). It has also been documented that Sand Forest species do not regenerate well in large gaps created by fire (Matthews 2006). However, the absence of disturbance, observed in Tshanini, shows that species distribution curves possibly change from Type 1 to Type 2 and bring the forest closer to an intermediate grain, the problem with the last statement being that it is contrary to grain theory (Everard *et al.* 1995). In the Intermediate Sand Forest therefore it appears that absence of disturbance is potentially as much of a problem as over-disturbance.

Large frequent gaps define large-scale disturbance that drive coarse-grained forests (Everard *et al.* 1994; Everard *et al.* 1995). In the event of such regular disturbance it has been hypothesised that forests could become coarse-grained as coarse-grained shade intolerant species out-compete the fine-grained shade tolerant species. The observation by Matthews (2006) on fire and Sand Forest could be likened to the process of transformation from fine-grained forest to a coarse-grained forest, except that in this case a woodland appears to replace the forest, although this author and several others have considered the closed woodlands of Tembe and Tshanini as forest-like units (Van Rensburg *et al.* 2000; Gaugris *et al.* 2004). Interesting questions would be to see whether under a continued small-scale disturbance the closed woodlands of this region would progress to a forest, would this forest be similar in species composition to Sand Forest, and whether the transition would follow a Short to Tall Sand Forest succession?



### **Note on the methodology**

The distinction between a full and a limited analysis used in the present study was based on an initial perception that regressions would work better at the full than the limited level. This somewhat cumbersome distinction proved true with regards to the regressions. However, the distinction proved particularly useful in separating the analysis in two parts that represented different tree dynamics. In terms of species evaluated in the limited analysis, it appears that the low number of individuals encountered was information in itself and it allowed a better understanding of the dynamics of the forest as a whole. While the statistical significance of the regressions is an important aspect of mathematical integrity, to overlook the species where regressions were not significant would have limited the ability to perceive patterns in the dynamics of this area. It appears therefore important to recommend that future studies in this field do not discard species with low abundance on the proviso that statistical significance was not met.

### **Conclusion**

The present study contradicts previous studies that classified Sand Forest as coarse to intermediate-grained forests (Everard *et al.* 1995; Gaugris and Van Rooyen In Press). These previous studies were based on considerably smaller sample sizes, and it appears that they did not pick up the regional levels of variations. The new perception presented here appears strongly supported by documented evidence and does explain Sand Forest character fairly well. The fine-grain character is a positive sign for Sand Forest conservation as it simplifies its management, and suggests that in Tembe and Tshanini, managers should concentrate on controlling the animal populations to ensure the presence of regular creation of small canopy gaps.

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